The Harvest Potential and Dynamics of Lake Trout Populations in Ontario

Lake Trout Synthesis
Populations Dynamics Working Group
1990

Ontario
Ministry of
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ABSTRACT

Payne, N.R., R.M. Korver, D.S. MacLennan, S.J. Nepszy, B.J. Shuter, T.J. Stewart, and E.R. Thomas. 1990. The harvest potential and dynamics of lake trout populations in Ontario. Lake Trout Synthesis, Ont. Min. Nat. Resour. Toronto. 72p.

A method for estimating the potential harvest of lake trout (*Salvelinus namaycush*) from a temperature-based volumetric measure of lake trout habitat is reformulated to increase its relevance to Ontario lakes and decrease its data requirements. Arguments are given for choosing this method over the past practice of partitioning the MEI yield. Provincial standards for lake trout length-at-age and weight-at-length are developed for use in comparative studies of lake trout populations and stress diagnosis. An "empirical" method of estimating von Bertalanffy growth parameters is introduced to deal with problems of bias in lake trout length and age data. Fecundity, age at maturity, and natural mortality data are compiled as partial descriptions of these aspects of lake trout dynamics. A method of estimating optimal fishing mortality and size at recruitment from growth parameters alone is described; tables are developed which facilitate its application to lake trout; and the relevance of such an application is tested. The method is derived from yield-per-recruit theory and embraces a widely-held marine fishing policy. An age-structured model which integrates knowledge concerning habitat limitations with knowledge about internal population behaviour is also used to estimate the level of fishing mortality consistent with maximum sustainable yield. Sustainable yield curves developed with the model are asymetric and show yields declining rapidly after a state of overexploitation is reached. Simulations of lake trout populations in "small", "medium" and "large" lakes suggest that populations in larger lakes are less vulnerable to overexploitation. Populations with total annual mortality rates (A) above 0.50 yr^{-1} are likely to be overexploited and in some instances even this level of mortality can be too high. Managers can reduce the vulnerability of lake trout populations to overexploitation by using size limits to delay the entry of year-classes into the fishery.

Keywords: lake trout, dynamics, synthesis, Ontario

INTRODUCTION

Potential fish yield from a lake is determined ultimately by energy and nutrient regimes and by lake morphometry. Attainment of that potential, however, depends on circumstances such as habitat constraints, species diversity and the status and dynamics of individual fish populations. The focus of this paper is the estimation of potential yield for lake trout (*Salvelinus namaycush*) and the role of population dynamics in the realization of that yield.

Yield theory for fish communities has advanced along two lines distinguished by the scientific approach taken. Empiricists have developed estimators of potential yield based on relationships between ecosystem attributes and observed yields for sets of lakes. At the same time, systems ecologists have estimated fish production (one measure of potential yield) using biological models that simulate processes operating at population or ecosystem levels. Empirical predictors, typified by the widely applied morphoedaphic index (Ryder et al. 1974), offer simplicity of use but only first-order predictions of potential yield. The more comprehensive ecosystem models, recently reviewed by Leach et al. (1987), represent important advances in theory, but refinement and application remain constrained by the availability and quality of input data. Understandably, empiric models remain in the forefront as management tools on the strength of their ease of use and the availability of requisite data.

Management for full resource utilization is facilitated when production potential can be estimated reliably at the level of individual fish species. However, most models predict yields for entire fish communities. Guidelines for partitioning potential yields estimated from the morphoedaphic index into individual species yields were developed empirically for Ontario lakes (Ontario Ministry of Natural Resources (OMNR) 1982), but the data were too variable and the guidelines too arbitrary to imbue much confidence in the results. More encouraging is the recent work of Christie and Regier (1988) which relates yields for four different species of fish to measures of optimal thermal habitat. We repeat and extend some of their analyses to enhance their lake trout model and facilitate its application to Ontario lakes.

Management of lake trout in Ontario is made difficult by the number and diversity of the lake trout lakes involved. Only a few can be studied intensively. A majority must be managed on the strength of temporally and typologically limited inventory and census data. In all instances, managers need to be able to assess the productive state of the lake trout resource, relative to its potential. Additionally, they need to know which of the factors operating are overriding and how best to restore or maintain healthy lake trout stocks and fisheries. The challenge is to develop, from the more intensive case history studies, scientific advice and a set of simple diagnostics which can be applied with minimal survey data to assess and manage the main body of provincial lake trout lakes.

Fish populations are increased in biomass by the entry of new individuals (recruitment) and by growth, and diminished by losses from natural death and exploitation. We proceed from a premise that the productive state of a lake trout stock can be characterized by variables which define these rates of population change. Various population parameters are examined individually as potential diagnostic features and in combination as an expression of our total understanding of the way in which lake trout populations behave.

Exploitation is the one non-biological process affecting yield and the process most amenable to control. Hence, single stock population models generally have as their objective the determination of the rate of fishing mortality which will maximize yield when the size at which fish are first harvested is known or has been fixed. Natural change rates which enter into such models, such as rates of growth, recruitment and natural mortality, are often treated as invariable, but in reality these rates and ultimately production do vary through time. This variability becomes increasingly important as maximum yields are approached because variability leads to uncertainty and uncertainty is akin to risk. Management advice must reflect this, with emphasis more on "sustainable" than on "maximum".

Density dependence accounts for some of the variability observed in population parameters. Reductions in fish numbers increase the individual's share of available resources, eliciting changes in growth, age at first maturity and perhaps fecundity. Such responses tend to be compensatory, acting to restore biomass that has been lost. The degree of compensatory change has been taken as a measure of exploitation stress and benchmarks have been proposed to facilitate lake comparisons (OMNR 1983). However, the utility of

this diagnostic approach depends on the validity of the standards and the amount of non-stress related variability which can be explained. These are areas in which we seek refinements.

We begin our analysis by relating the potential harvest of lake trout to a measure of habitat availability based on the concept of a fundamental thermal niche (Magnuson et al. 1979). From this extrinsic determinant of harvest potential, we go to several intrinsic characteristics of lake trout populations which affect their capacity to increase, namely to growth rate, time to maturity, fecundity and natural mortality rate. Beyond that point, we examine two ways by which management guidelines can be developed from the preceding descriptors of lake trout population biology. The first arises out of yield-per-recruit theory and requires only growth and mortality information for defining optimal controls on fishing. The second approach involves a population model which integrates essentially all of our information on lake trout productivity. With it, differences in optimal fishing mortality rate and vulnerability to overexploitation with differing lake size are explored.

With little exception, the terms harvest and yield are used throughout this report in the following sense: harvest is the total weight of fish kept per unit time (kg yr^{-1}); and yield is the total weight of fish kept per unit of surface area and time (kg ha^{-1} yr^{-1}). The exception is the expression "maximum sustainable yield" (MSY), which is a concept inferring maximum realized production (whether expressed as yield or harvest). We continue to use it in this generic sense. Hence, if the units that follow are in kg yr^{-1}, it might be read as maximum sustainable harvest.

ESTIMATING POTENTIAL HARVEST FOR LAKE TROUT

Christie and Regier (1988) defined some thermal bounds for fish habitat, developed some simple measures of this "thermal space" and searched for relationships between those measures and sustainable harvest. Their study encompassed four species of fish, lake trout included. For each species, they selected a 4°C temperature range as an approximation of the optimal thermal habitat (8-12°C in the case of lake trout). For the summer period (June-September), the volume of water bounded by these temperatures was calculated from vertical temperature profiles, averaged over 10 day intervals, and from measures of the total area of the lake at given depths. These volumes (cubic hectometres per 10 d) were summed over the entire summer period to produce a final value termed the thermal habitat volume (THV). Across the 15 large lakes (18,900 - 8,241,400 ha) in their lake trout data set, they found that 86% of the variation in lake trout harvest (kg yr^{-1}) was explained by THV, 10% more than explained by volume alone.

Nearly one-half of Ontario lake trout lakes are less than 200 ha (Martin and Olver 1976) and far outside the size range of lakes in Christie and Regier's data set. In theory, the thermal habitat model for estimating potential harvest, because of its physiological basis, should still apply. Nevertheless, extrapolation of that estimator to such small Ontario lakes was considered ill-advised without further analysis. Therefore, we have extended Christie and Regier's analysis to include Ontario lake trout lakes meeting the data requirements and population stability criteria. As well, we have reanalyzed Christie and Regier's original data to determine if THVs based on fewer temperature measurements would provide equivalent predictive power.

For the reanalysis, we initially considered both maximum and minimum estimates of THV, and THV over some stable period during the summer as potential surrogates for full-season measures. However, wide variation among lakes in the seasonal pattern of THVs introduced inconsistencies in the minima and maxima and they received no further consideration. Variation was least (CV = 45%) in the three mid-summer periods corresponding approximately to the month of July (Fig. 1). The reanalysis was therefore performed using the geometric mean of July THVs. The resultant regression accounted for 89% of the

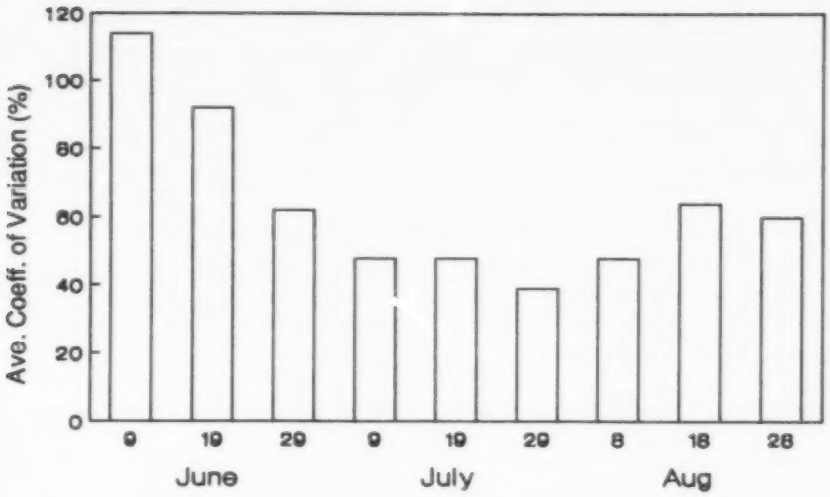

Fig. 1. Seasonal variation in thermal habitat volume for the first 15 lakes in Table 2. Dates are day one of 10 day periods over which temperature data were aggregated. Coefficients of variation for each time interval were determined for between year variability within lakes and averaged over all lakes.

variation in lake trout harvest, with THV explaining 13% more than lake volume alone. Removing the earlier and later months, with their greater between-year variability in temperature profiles, thus seems to have increased the precision of the thermal habitat measure without destroying its relevance.

This result made Ontario lakes with an extended harvest record and July temperature profiles eligible for addition to Christie and Regier's original data set. But only four such lakes were found. This led to consideration of two additional lakes (Christman and Chiblow/Denman) which, on the basis of similar (CV = 32% and 1.5%) THV estimates for June and August, were judged to have relatively stable summer thermal regimes. This is not uncommon in small lakes. Acceptance of a broadening of the sampling "window" in these two instances thus was not thought to unduly compromise precision, nor the concept of a July standard. Final acceptance of the now six candidate lakes depended on stable harvest and population attributes having been maintained under a history of moderate to heavy fishing pressure. As a test of this, the six lakes (Table 1) were examined by simple regression analysis for any trends in harvest, fishing effort, total mortality rate, and growth (measured as length at age 6) that might point to instability. One, Wakwekobi Lake, was rejected on

Table 1. Summary harvest, effort, and lake trout population attributes for candidate lakes for potential yield analysis. Coefficients of variation are in brackets. Statistically significant ($p < .01$) increasing or decreasing trends are indicated by a + or - superscript.

Lake	Study years	Harvest ($kg\ yr^{-1}$)	Effort (angler-hr)	Total mortality	Length at age 6	Mean age
Flack	1969-83	1285 (23.5)	7327 (14.0)	0.71 (15.2)	400 (4.5)+	5.4 (4.9)
Opeongo	1965-79	4005 (27.9)	15988 (27.4)+	0.36 (19.8)	367 (2.3)	7.6 (6.7)
Chiblow/Denman	1967-84	1570 (55.2)	8583 (34.4)	0.72 (15.9)	433 (2.7)	6.1 (4.3)
Wakwekobi	1967-84	1001 (51.6)+	8320 (34.4)	0.58 (51.7)	428 (12.5)	6.6 (10.8)+
Christman	1968-80	94 (65.7)	875 (51.3)	0.64 (11.7)	432 (8.9)	5.4 (7.3)
Bone	1968-84	256 (37.7)	3313 (29.6)+	0.77 (11.4)	316 (39.9)	4.4 (6.1)

Table 2. Summary of parameter values used for generating lake trout harvest models. The first 15 lakes are the set of lake trout lakes used by Christie and Regier (1988). The last five are our additions of Ontario lakes.

Lake	Harvest ($kg\ yr^{-1}$)	Area (ha)	Yield ($kg^{-1}ha^{-1}yr^{-1}$)	Volume (cu hm)	July THV (cu hm)
Lake Superior	1895500	8241400	0.23	12230000	1011766
Lake Michigan	3248900	5801600	0.56	4908000	471483
Lake Huron	1499700	4165900	0.36	2791000	264505
Great Slave	1003200	2538200	0.40	1574000	114102
Lake Ontario	311600	1947700	0.16	1637000	118290
Georgian Bay	660100	1375200	0.48	660000	102290
Lake Erie	50000	623700	0.08	151700	19822
Reindeer	278600	556900	0.50	94700	25866
North Channel (L. Huron)	254800	455000	0.56	88000	21672
Lake Nipigon	130900	448100	0.29	221500	24638
Lake of the Woods	7800	356900	0.02	28200	947
Wollaston	159200	206200	0.77	42500	11785
Lake La Ronge	64000	130700	0.49	17700	2865
Cree	100600	115200	0.87	17200	4472
Amisk	13400	32100	0.42	4200	895
Opeongo	4005	5894	0.68	755	112
Chiblow/Denman	1570	2675	0.59	621	62
Flack	1285	951	1.30	198	27
Bone	256	121	3.00	9	0.8
Christman	94	59	1.00	4	0.5

the basis of trends detected in three of these variables. Opeongo and Bone lakes, with increasing effort but stable yield, and Flack Lake, with increasing growth but relatively stable yield, were accepted. The addition of five smaller lakes to the original 15 extended the range of lake areas in the final set from 59 ha to 8.2 x 10^6 ha (Table 2).

For the five new lakes, individual July temperature profiles (or equivalents) were interpolated linearly to 2.5 m depth intervals and averaged across depths. The resulting single profile for each lake was then combined with interpolated area-at-depth data to calculate the volume of water between 8 - 12°C (see Appendix A). Simple linear regression analysis of lake trout harvest on lake area, lake volume, and July THV was performed after $\log_{10}$ transformation of all data. The resultant coefficients of determination (r^2) for all variables were higher than those returned from Christie and Regier's original analysis and our reanalysis of their data using July THVs. July THV proved the best predictor, explaining 97% of the variation in lake trout harvests over the expanded lake set (Fig. 2, Table 3). In neither Christie and Regier's original analysis (for lake trout) nor our reanalysis were the correlation coefficients (r) from the three single independent variable regressions (area,

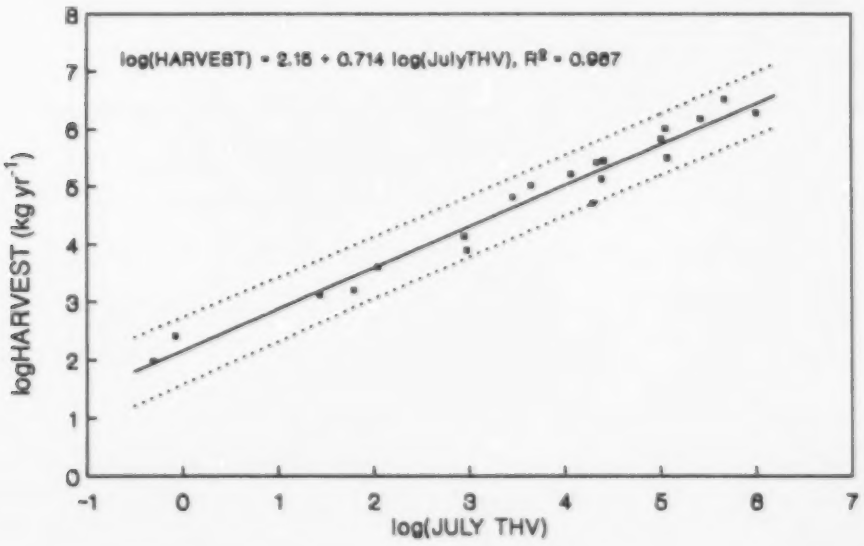

Fig. 2. Relationship between sustained harvest (kg yr^{-1}) of lake trout and thermal habitat volume (THV, hm^3). The 95% confidence limits (light lines) are applicable when indicated equation is used to predict harvest for a particular lake.

Table 3. Coefficients of determination (r^2) for the regression of lake trout harvest values on selected independent variables (log transformed values). See text for an explanation of the different analyses.

	Area	Volume	THV
Christie and Regier (1988)	0.706	0.758	0.859
Reduced model (July THV)	0.706	0.758	0.892
Expanded data set (July THV)	0.923	0.934	0.967

volume, THV) significantly different (Fisher's z-transformation $p > .05$). However, it has been shown by multiple regression that the thermal habitat component substantially improves the amount of variation explained (Christie and Regier 1988).

We recommend July THV as an alternate basis for predicting the potential harvest of lake trout from Ontario lakes on the strength of its specificity to that species and its minimal data requirements (e.g. lake inventory data), but also to enable its strengths and weaknesses to be further explored through use. The formulation to be used is:

$$\log_{10}H = 2.15 + 0.714 \log_{10}(\text{July THV}) \qquad [1]$$

where H = potential harvest (kg yr^{-1}) and July THV = thermal habitat volume calculated from July temperature data. Potential yield (kg ha^{-1} yr^{-1}) can be easily obtained by dividing by area. To our recommendation we attach the following caveats:

(a) Managers using the THV model should not be deceived into unrealistic expectations of precision by the high coefficient of determination ($r^2 = 0.97$), which owes much to a very large area effect ($r^2 = 0.92$). Instead, they should note the 95% confidence limits around the estimate of harvest predicted by the model. For example, a lake with a THV of 1.0 hm^3 (log THV = 0), typical of the smallest lakes in the data set (Bone, Christman), would have an estimated potential harvest of 141 kg yr^{-1} with confidence limits at 37.4 and 535, a span of roughly an order of magnitude. This seemingly wide range should not come as a complete surprise given the variability in fisheries data in general. The truth is that managers must accept high uncertainty in information used to make decisions and to learn to think in terms of risks involved in, say, managing at a particular level of harvest.

Over the much more limited range of lake sizes found inland in Ontario, the area effect noted above will be less pronounced and the effect of other variables, such as the edaphic variable TDS, will be more evident. Nevertheless, we would expect habitat quantity (THV)

to overwhelm habitat quality (as measured by TDS) as the major determinant of whole lake harvest, because of the generally low variability in the latter across most lake trout lakes in Ontario (Martin and Olver 1976).

(b) Caution is required when applying the thermal habitat model to small (< 100 ha) lakes. Apart from being inadequately represented in the test data set, such lakes tend to have low species diversity, few, if any, competing predators, dense populations of planktivorous/benthivorous lake trout and relatively high yields (Carl et al. 1990). As well, the smaller the lake, the greater the likelihood that critical elements of habitat other than the temperature regime will become limiting. Depending on shape, small lakes may have short fetch, shallow mixing, and little cleansing by waves of potential spawning areas.

(c) Factors other than temperature can restrict the amount of optimal habitat and allowance must be made for any known to be limiting. For example, with severe oxygen depletion, an oxygen deficit may make some part of the THV inhospitable. In such cases, the lower oxygen threshold for optimal lake trout habitat (6 mg L^{-1}, MacLean et al. 1990) will be encountered before the the lower temperature boundary ($8^{o}C$) is reached and the depth of the former, not the latter, should be used in the calculation of optimal habitat volume.

(d) Finally, any potential harvest estimate will be affected by the representativeness of the temperature data used. Multiple years of temperature data are always preferable to data from a single season, even though the latter are sufficient to produce an estimate.

GROWTH

Growth is one of the more variable and sensitive aspects of lake trout dynamics, responding early to biotic and abiotic changes in the environment and also to changes in lake trout density within relatively stable environments. This broad sensitivity to change makes growth useful for monitoring net alteration between this species and its environment, but confounds any attempt to isolate the effect of a single variable.

Change in growth, as it relates to density change and intraspecific competition, has been taken as a qualified measure of the stress of exploitation (OMNR 1983). The standard for comparison in the case of the earlier OMNR application took the form of a graphic

representation of average provincial lake trout growth and corresponding mathematically derived growth coefficients. We have updated this and added a weight-length standard.

Only mean values for length-at-age and weight-at-age were available in the "summary" data base used for these growth analyses. It is unlikely that the lack of original sample data has seriously prejudiced the results, but it has prevented any consideration of variance.

LENGTH-AGE RELATIONSHIP

Fish growth may be represented in many ways, but in this section we shall concern ourselves with the relationship between length and age. In general, the von Bertalanffy growth equation gives a reasonable description of this relationship and should be applicable to lake trout considering their age range and ecology (Casselman 1983). The most commonly used formulation of the equation is

$$L_t = L_\infty(1-e^{-K(t-t_0)}) \qquad [2]$$

where L_t is the mean length of the fish at age t (we use fork length in cm and age in years), L_∞ is the asymptotic length of fish (i.e. the extrapolated mean length at infinite age), K represents the fraction by which the gap between L_t and L_∞ is closed each year (units yr^{-1}), and t_0 is the extrapolated age at which L_t is zero. These parameters are important, not only for predicting size at age for a given population, but also for use as inputs to models that we introduce later.

Proper representation of growth must be based on unbiased estimates of size and age (see Lester et al. 1990). However, techniques used for growth assessment of lake trout in Ontario result in biases for both size and age. These biases are summarized in Fig. 3. The length-at-age of young fish is often overestimated due to capture and retention by anglers of the largest fish in year-classes not fully recruited to the fishery. For older fish, another problem is apparent. The vast majority of age assessments in the province have been done using scales. This results in progressively greater underestimation of true age as fish get older (Casselman 1983). In addition, small sample sizes (for older age groups in particular) often lead to very low precision for estimates of mean size at age. The consequence of these problems is that the von Bertalanffy model cannot always be fitted, or if it can, parameter values are quite unrealistic (see OMNR 1983).

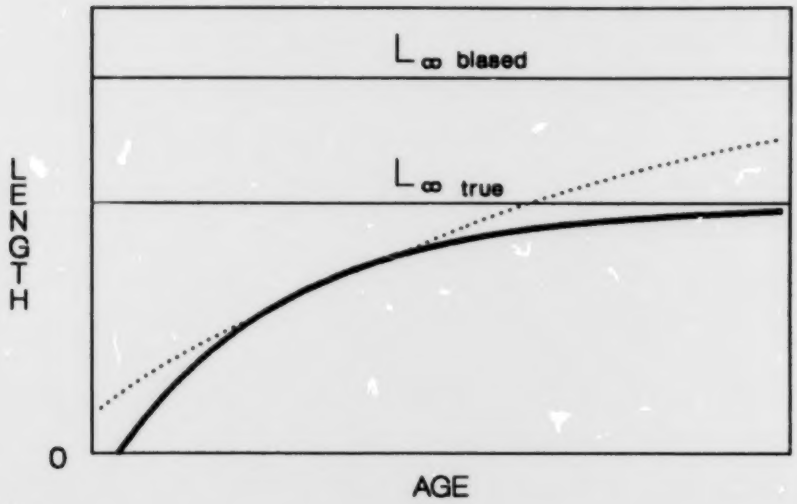

Fig. 3. Diagram showing the effect of bias on the estimation of von Bertalanffy parameters for lake trout. The solid line represents a von Bertalanffy curve fitted for a hypothetical population where mean length and age are accurately sampled. The dotted line shows how the curve might be changed due to sampling bias. Selection for large fish at young ages results in overestimation of length at age. Scale ageing tends to underestimate true age to a progressively greater degree as fish get older, making the mean size-at-age for old fish appear larger than it actually is. If a von Bertalanffy fit is even possible, extrapolation with biased data can give an unrealistically high estimate of L_∞, with an associated lower value for K.

In the following paragraphs, we provide a method that allows approximation of von Bertalanffy parameters from data having the above-mentioned inadequacies. The method is then used to develop an updated summary of lake trout growth. We stress that the technique employed is not a final solution; an overhaul of current sampling practices might be.

The parameters of the length-age equation are merely values derived from the mathematical fitting of a particular function to the observed data. Therefore, their biological interpretation requires care (see e.g. Schnute and Fournier 1980; Moreau 1987), especially when bias is suspected. L_∞ is not necessarily a reliable estimate of the longest length or slightly beyond; K does not necessarily tell you whether the population is fast or slow growing; and it is hard to see why t_0 should not be zero. The model merely predicts mean length over the range of ages reasonably represented by the data. Extrapolation beyond this range, to L_∞ for example, is tenuous at best. Alternate parameterizations of the von Bertalanffy equation (Schnute amd Fournier 1980; Ratkowsky 1986) ease the problem of

extrapolation and interpretation, but do not assist in getting more realistic estimates from biased data.

The most obvious effect of fitting the von Bertalanffy model to biased data (as in Fig. 3) is that L_∞ may be grossly overestimated (OMNR 1983). If, however, we redefine L_∞ to be some empirical measure of the maximum length of fish, call it L_∞', we might expect that measure to be closer to reality, provided old fish remain in the population. In addition, L_∞' becomes independent of the ageing of old fish and is closer to what intuition tells us L_∞' should be.

Setting L_∞ to L_∞' will constrain the model. If we further constrain it by setting t_0 to zero, thus countering bias in the youngest age classes, only K, which we now will call K′, remains to be estimated. With L_∞ fixed, the von Bertalanffy equation can be rearranged into the form of a linear regression

$$-\ln(1-\frac{L_t}{L_\infty'}) = Kt - Kt_0 \qquad [3]$$

where

$$y = -\ln(1-\frac{L_t}{L_\infty'})$$

and

$$x = t$$

The slope of the line when forced through the origin (equivalent to setting t_0 to zero) gives an estimate of K′. A derivation of this relationship is found in Pauly (1984, p. 29; we ignore Pauly's parameter D).

We applied this empirical method to a 47-lake data set consisting of mean fork length -at-age and associated sample sizes (Appendix Table B). First, mean lengths were ranked by length rather than age. The geometric mean, weighted by sample size, of the longest lengths comprising 5% of the total sample or 10 fish, whichever was less, was used as the estimate of L_∞'. A sample of two fish was set as the absolute minimum for estimating L_∞', and several lakes were rejected for not meeting even this weak criterion. Only mean lengths

for ages 4 through 7 were used to estimate K′. Younger age groups were judged to be too susceptible to gear selection and often were missing from samples. Age 7 was taken as the maximum for reasonably reliable scale ageing (J. Casselman, OMNR, Glenora Fisheries Station, R.R. 4, Picton, Ont. K0K 2T0, pers. comm.), even though biases begin to arise around age 6 (Casselman 1983; Ball 1988). Regressions were weighted by sample size.

As a check on the validity of this method, parameter values thus obtained were compared with those obtained by conventional non-linear estimation (Table 4). For this purpose, we used available data from 12 lakes where ages had been determined by the more reliable otolith method. The non-linear fits (using RS/1 FIT FUNCTION routine and the full range of age-length data, weighted by sample size) were forced through the origin ($t_0 = 0$). In five instances, L_∞' fell outside the confidence intervals constructed for L_∞ and on that basis the differences were considered significant. K′ departed from K by more than its confidence interval in three instances. This seemingly large number of significant differences can be explained in several ways that are largely independent of the two estimation techniques:

(a) The test used here is quite conservative as it assumes (incorrectly) that the empirical estimates are without error. Some differences, such as those for L_∞ for Pickerel and Robinson lakes, would become insignificant with even a very small error in the empirical

Table 4. Comparison of von Bertalanffy parameters from the empirical method and nonlinear estimation for 12 lakes where lake trout were aged by otoliths. SE = standard error; (LCL, UCL) = 95% confidence interval; Y/N = yes/no; lengths in cm.

		Nonlinear estimates						Nonlinear estimates				
Lake name	L_∞'	L_∞	SE	LCL	UCL	Sign. Diff	K′	K	SE	LCL	UCL	Sign. Diff
Squeers	55.0	48.5	.95	46.5	50.5	Y	0.137	0.171	0.0076	0.155	0.187	Y
Greenwater	58.4	60.8	2.48	55.5	66.0	N	0.162	0.155	0.0126	0.128	0.181	N
Little Gull	59.3	59.3	3.73	51.3	67.2	N	0.137	0.144	0.0190	0.103	0.184	N
Lake of the Woods	81.5	115.4	9.02	96.0	134.7	Y	0.137	0.085	0.0101	0.063	0.106	Y
Pickerel	67.0	71.9	2.25	67.2	76.5	Y	0.121	0.112	0.0066	0.098	0.125	N
Robinson	61.6	59.0	1.17	56.5	61.4	Y	0.164	0.160	0.0102	0.138	0.181	N
Little Joe	59.9	60.7	4.26	51.4	69.9	N	0.207	0.230	0.0370	0.150	0.311	N
South Otterskin	60.7	68.5	1.45	65.3	71.7	Y	0.210	0.167	0.0073	0.151	0.184	Y
Islets	52.7	53.2	9.45	51.1	55.2	N	0.229	0.238	0.0141	0.207	0.268	N
Burnt Island	54.2	58.6	3.49	50.9	66.2	N	0.160	0.148	0.0173	0.110	0.186	N
Greenwich	43.7	43.8	1.29	41.0	46.5	N	0.242	0.238	0.0206	0.193	0.282	N
Lock Erne	60.2	73.8	6.55	59.5	88..1	N	0.154	0.124	0.0196	0.082	0.167	N

estimates. It should be stressed that any comparison involving extrapolated values will be lacking in rigor.

(b) Differences for Squeers Lake were largely attributable to the use of mean length-at-age data, where only age groups totalling to five of the 10 fish required by the empirical method were included in the calculation of L_{∞}' (see data in Appendix Table B). The next largest age group, which would have raised the sample to 20 fish, would have resulted in no statistical difference. Only lengths from age groups giving a sample size closest to that specified for the empirical method were included; obviously it would be best to use individual fish.

(c) For Lake of the Woods, neither method worked particularly well. The non-linear approach overestimated length-at-age for old fish (as observed), while the empirical method produced underestimates. The best estimates of K and L_{∞} should be somewhere in between. For South Otterskin Lake, the empirically fitted line again fell above observed lengths for old fish.

(d) Agreement between the two methods is largely dependent on the estimation of L_{∞}'. With L_{∞}' set to the value found by non-linear estimation, none of the differences found for K even approach significance (data not shown). Estimates of L_{∞}' would be improved if based on data for individual fish, rather than on mean length-at-age. This change might also remove a slight tendency for the fitted line to fall below actual data points for old fish.

Parameter values (L_{∞}' and K') describing lake trout growth for 47 provincial lakes are listed in Appendix Table B and summarized in Fig. 4. The figure shows values calculated using a collection of techniques referred to as exploratory data analysis (Velleman and Hoaglin 1981). The middle (solid) line represents the median estimated fork length-at-age, rather than the mean. The two lines immediately below and above the median line are the so-called "hinge" values, which are approximately equivalent to 25- and 75-percentiles, and the outside lines represent minimum and maximum values. The data set has been reduced by excluding lakes having outlying or "outside" values (more than 1.5 times the hinge-spread outside the hinges; Velleman and Hoaglin 1981). These outside values were all for lakes seeming to have unusually fast growth, and were quite far removed from the majority of the data. The thick lines connect the actual mean size at ages 4 through 7 (used to calculate K').

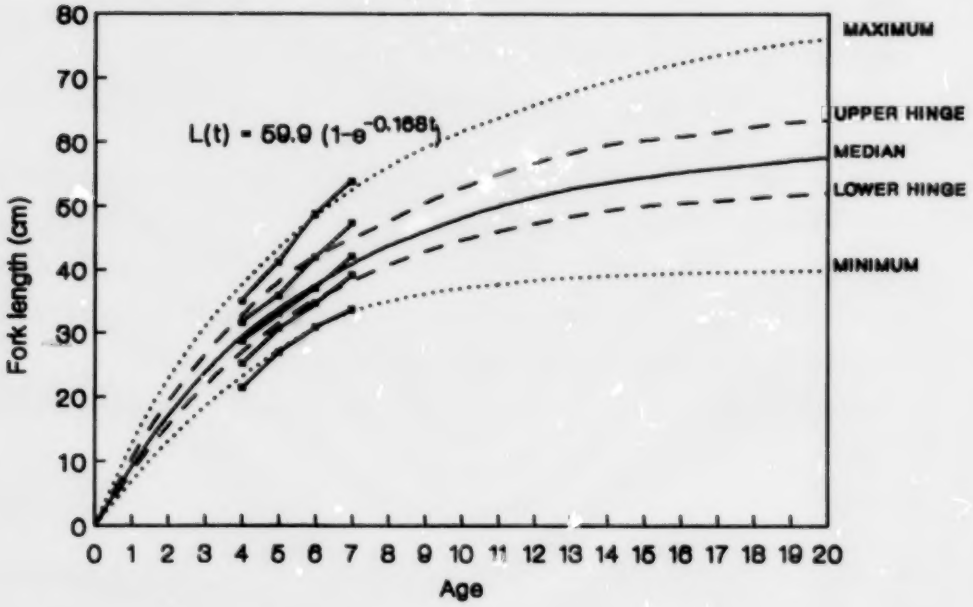
MAXIMUM
UPPER HINGE
MEDIAN
LOWER HINGE
MINIMUM
L(t) = 59.9 (1-e^-0.168t)
Fork length (cm)
Age
0 10 20 30 40 50 60 70 80
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20

Fig.4. Summary of estimated fork length (cm)-at-age for lake trout in 47 Ontario lakes. Von Bertalanffy parameters (L_∞' and K') were calculated for each lake. The median, hinges, maximum and minimum values were found for the resulting lengths estimated for each age. The four areas demarcated by the lines drawn on the graph each represent approximately one-quarter of the lakes. The thick lines show equivalent values for actual mean length at ages 4-7 (used to calculate K'). Median values for L_∞' and K' were used to generate the "standard" equation for the province (top-left corner).

Fig. 4 is useful for management purposes in that it offers a simple means for relating growth in a particular lake to the spectrum of provincial lake trout growth. At the same time, managers should be wary of the fact that it does not consider within lake error associated with length measurements and age determinations for the age groups used.

Median values for L_∞' and K' were 59.9 cm and 0.168, respectively. This represents a substantial difference from the results of an earlier growth analysis (OMNR 1983); the asymptotic size found then was 145.25 cm, over twice the current estimate. Much, if not all of this difference is likely attributable to the different approach to parameter estimation.

Lake trout lakes in the province are readily separated into three geographic zones on the basis of clustering: one comprising the northwestern and north central regions; one consisting of the northern and northeastern regions; and one encompassing the remaining southern regions (Martin and Olver 1976). An examination of growth parameters for

differences between these zones (ANOVA) and also with latitude (regression) failed to establish that any exist. This is not proof of similarity, but does imply that any zonal or latitudinal differences are small in relation to differences among individual lakes.

Lake specific factors may explain more variability in growth. Von Bertalanffy parameters were found to correlate with lake area (Fig. 5). Log_{10} transformed values for area explained 41% of the variation in L_∞' and 20% of the variation in K′. Hence, there is some evidence that fish grow to larger asymptotic size in large lakes. The reduction in K with lake area is not likely a reflection of slower growth rates, but merely the effect of correlation with L_∞ (Gallucci and Quinn 1979; Lester et al. 1990).

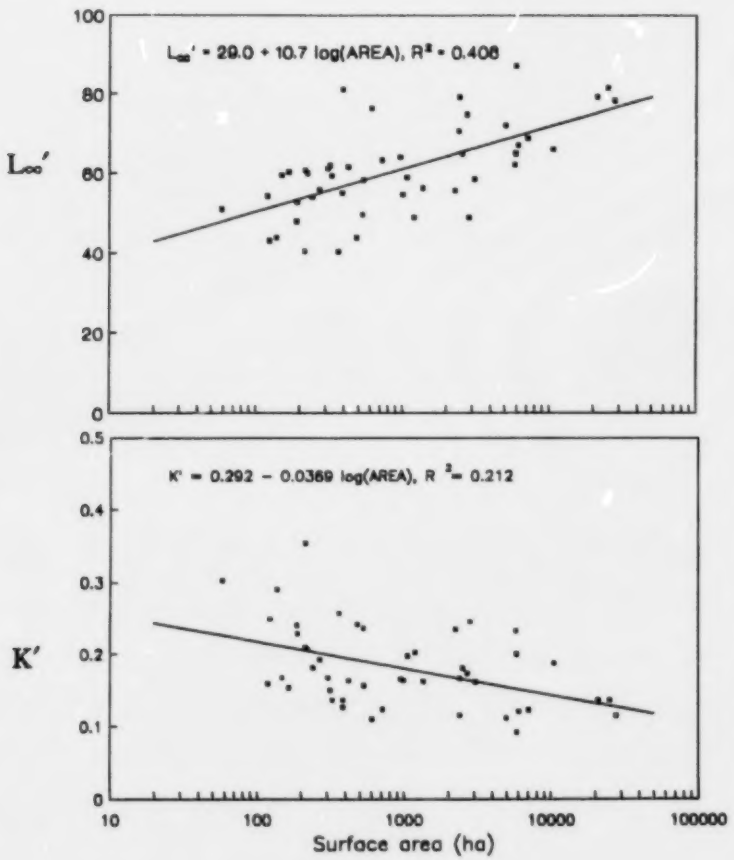

Fig. 5. Relationship between lake size and estimated von Bertalanffy paramaters (L_∞' and K′) for 47 Ontario lakes.

To summarize briefly, biases in length-at-age data complicate analyses of growth in lake trout. To contend with this problem, we have introduced an empirical method of estimating von Bertalanffy growth parameters which draws on data from a reduced age range over which the bias is likely to be minimal or absent. A validation test has shown that the method produces results reasonably consistent with those obtainable using the conventional non-linear estimation procedure with data considered relatively complete and accurate. With this as background, the method has been used in conjuction with a set of provincial lakes to describe lake trout growth in the province.

The significance of these results to managers can be summed up as follows:

(a) The empirical method of von Bertalanffy parameter estimation will produce results that are more realistic than those obtained with methods that wrongly assume unbiased length-at-age data. It is easily applied (see example in Appendix C) and removes the requirement for determining ages for older fish (>age 7). It should be considered only as an interim solution to the bias problem, as the greater need is to refine sampling methodologies. While current sampling methods prevail, any estimates of von Bertalanffy parameters should be viewed with a degree of scepticism.

(b) The median values for fork length-at-age (Fig. 4), given by the equation

$$L_t = 59.9(1 - e^{-0.168t}) \qquad [4]$$

where t = age in years and L_t = fork length in cm at age, can be taken as one standard against which lake trout growth for individual lakes may be compared. Range values and "hinge" values in Fig. 4 will assist in positioning the growth of a lake trout stock in the provincial spectrum. A caution is that past growth curves from biased data not be used in such comparisons. Where bias is suspected, new von Bertalanffy parameters should be obtained by the empirical method described. As well, there are two aspects of the length-age standard about which users should be cognizant. First, the possible existence of different growth stanzas resulting from dietary change has been overlooked as a consequence of fitting a single equation to the data and limiting the range of ages used. Second, by using summary data, sampling error at the individual lake level has been essentially ignored.

WEIGHT-LENGTH RELATIONSHIP

The relationship between weight and length reflects the state of well-being of individual fish in a population. Like growth rate, it is an indicator of environmental and density change. But unlike growth rate, its utility as a diagnostic tool is not confounded by age assessment problems. Sampling gear selectivity remains a source of bias, but more so with gill nets, which select on the basis of girth, than with angling.

We derived a provincial length-specific weight standard using data from various years for 23 Ontario lakes (Appendix Table D). The relationship defined is in the form

$$W = aL^b \qquad [5]$$

where W = weight in g, L = fork length in mm, and a and b are derived parameters.

The parameters a and b were estimated for each lake by least square linear regression of $\log_{10}$ transformed mean weight- and length-at-age using the function:

$$\log W = \log a + b \log L \qquad [6]$$

Means were again used because data from individual fish were unavailable. This reduced variability among the final pairs of values and contributed to correlation coefficients (r) of nearly 1.0. With r so high, recourse to the functional or GM form of regression (Ricker 1973), normally employed when both variates are subject to measurement error, was unnecessary.

Lakes were included in the analysis if represented by length-weight data from 50 or more fish of widely varying age (with one exception where the data were suspect). From these, age groups were deleted if the sample size was less than four as they typically appeared as outliers. Remaining age groups were given equal weighting. The final data and resultant a and b values are listed in Appendix Table D.

Data used came from the winter, spring or summer seasons of the year, except for Flack Lake for which there was a fall sample. Differences in the parameters of the weight-length relationship for lake trout may occur over these three seasons but were not visible in a plot

of our results (not shown). However, *b* values might be expected to increase slightly in the fall period when gonadal weight is maximal.

The derived *a* and *b* values were used to calculate weights at a series of standard fork lengths for each of the 23 lakes (Table 5). Summary statistics from these appear at the foot of Table 5 and graphically in Fig. 6. Graphical (discontinuous variables) and regression (continuous variables) analyses failed to reveal an influence on the parameter *b* at a standard length of 400 mm by any of the following lake variables: latitude, surface area, mean depth, MEI, potential yield, and fish community type (results not shown). Likewise, superimposed plots of mean weight- and length-at-age for each of the three previously defined geographic zones (page 15) showed no perceptible geographic difference. The summary data set from which weight-length data were drawn rarely provided sex or maturity information. Thus, we were unable to assess the influence of either of these states. As well, the lack of useful quantitative measures of stress prevented any analysis for stress effects.

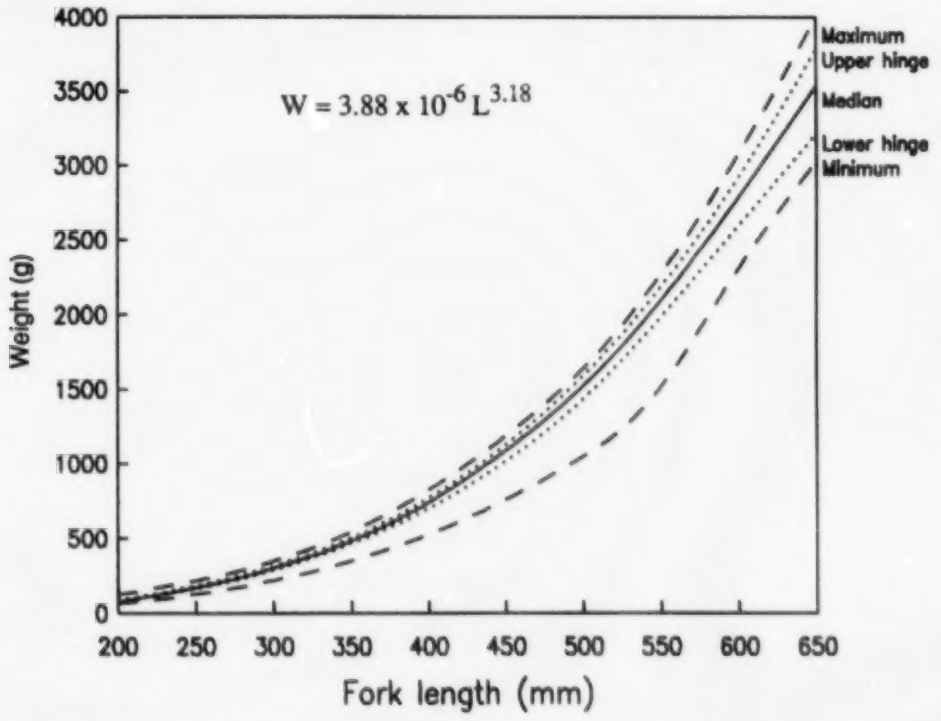

Fig.6. Weight-length relationship for lake trout drawn from summary statistics in Table 5. The four areas demarcated by lines drawn on the graph each represent one-quarter of the lakes. The "standard" weight-length equation is shown in the upper-left corner.

Table 5. Parameter values "a" and "b" for the lake trout weight-length function, calculated weight at selected fork lengths for 23 lakes in Ontario, and summary statistics for all lakes combined. Weights in small print are for non-observed lengths and were exclued from summary statistics.

Lake name	Weight-length relation			Calculated weight at standard fork-lengths						
	"a"x10^{-6}	"b"	r^2	200	250	300	350	400	500	600
Wollaston	375.61	2.40	.997	124	212	328	475	655	1118	1732
Dickey	248.52	2.47	.988	123	213	335	491	683	1186	1863
Gong	10.04	3.03	.996	93	182	316	504	756	1485	2578
Greenwater	7.47	3.09	.989	95	190	333	537	810	1614	2835
Lake Joseph	6.71	3.08	.995	81	160	280	451	679	1350	2365
Chiblow	6.00	3.10	.996	81	162	286	461	697	1392	2450
Pickerel	5.57	3.12	.995	86	172	305	493	749	1503	2657
Christman	4.79	3.15	.998	86	174	309	503	766	1549	2752
Ranger	4.42	3.10	.996	61	121	214	345	522	1043	1837
Greenwich	4.07	3.17	.998	80	162	290	472	721	1463	2607
Bone	4.03	3.18	1.000	83	170	303	495	756	1537	2745
Islets	3.88	3.17	.997	77	156	277	452	691	1402	2499
Goulais	3.54	3.20	.993	84	171	307	503	771	1576	2827
L. of the Woods	3.26	3.21	.999	78	159	285	467	716	1464	2626
Burnt Island	2.78	3.23	.998	76	157	283	466	717	1476	2660
Lake Opeongo	2.60	3.25	.997	79	164	297	490	757	1565	2831
Flack Lake	2.35	3.28	.996	83	172	312	518	803	1668	3033
Little Joe	1.89	3.31	.999	77	160	293	488	758	1586	2898
S. Otterskin	1.35	3.36	1.000	72	153	283	475	744	1574	2904
Lach Erne	1.18	3.37	.998	68	145	268	451	708	1503	2780
Adelaide	.85	3.42	.998	63	135	252	427	674	1446	2697
Semiwite	.82	3.44	.998	67	145	272	462	732	1577	2952
Wakwekobi	.59	3.50	.999	65	143	270	462	737	1608	3041
All lakes										
Mean	4.12	3.18	.99	84	166	292	473	720	1484	2730
Median:	3.88	3.18	---	80	162	292	475	727	1503	2766
Minimum:	.59	2.40	---	63	121	214	345	522	1043	2365
Maximum:	375.	3.50	---	124	213	335	810	1614	1614	3041
25% Quartile:	1.89	3.10	---	78	156	279	689	1413	1413	2590
75% Quartile:	6.00	3.31	---	91	174	310	758	1576	1576	2881

We propose that the median line in Fig. 6, represented by the equation

$$W = 3.88 \times 10^{-6} L^{3.18} \qquad [7]$$

be taken as a provincial weight-length standard for the purpose of comparisons.

Apart from establishing standards that may be used in stress diagnosis, this and the preceding section on length-at-age offer a basis for assigning default values relating fish size to age for initializing population models when lake specific data are unavailable.

REPRODUCTIVE POTENTIAL

In this section, we confine our attention to maturation schedules, which weigh heavily in calculations of spawning stock size, and to fecundity, which is required to estimate potential egg deposition. The more central issue, namely the relationship between adult stock size and recruitment, is dealt with in a later modelling section.

MATURITY

The limited reported information from Ontario lakes on the age and length of lake trout at maturity is presented in Table 6. These data are lacking in comparability and therefore offer more a partial description of maturation schedules than an opportunity for analysis. In southern Ontario lakes, the tendency is for female lake trout to begin to mature at age 5, half to be mature at age 7, and all to be mature at age 8, although individual lakes vary from this pattern. On average, maturity occurs about two years later in northern Ontario, although again there are exceptions. The similarity between north and south in the values for 50% maturity is likely a reflection of the small number of lakes in the sample and their location in the distribution. More information on maturity and frequency of spawning is needed before any of the questions relating to this important aspect of the life history of lake trout can be satisfactorily answered.

FECUNDITY

Estimates of absolute (eggs per female) and relative (eggs per kg) fecundity of lake trout for a small set of Ontario lakes are given in Table 7. Absolute fecundities reflect the wide

Table 6. Age and length (fork length in mm in parentheses) at maturity of female lake trout from various lakes in Ontario.

Lake	First Mature		50% mature		90 - 100% mature		Source
Southern Ontario							
Opeongo	5	(380)	7-8		9-10		Martin & Fry (1973)
Red Rock	7	(450)					Martin (1951, 1956)
Louisa	6	(330)	7		8		"
"	6	(379)			8	(437)	Hicks (1985)
Smoke	5	(307)			8	(511)	Hicks 1985)
Lavielle	6	(382)			8	(493)	"
Drag	5.8-6.5						Hoyle & Stewart (1987)
Dickey	4.4-5.3						"
Twelve Mile	5.7-6.2						"
Big Clear	5						Paleczny & MacLean (1987)
Big Rideau	5						"
Charleston	5						"
Big Porcupine	5				7		Ball (1988)
Nanikani	4				7		"
Sherborne	5				9		"
Kimball					7		"
Bonnechere	5				7		"
Northern Ontario							
Bone	5						Bernier (1976)
Christman	4	(383)	6	(395)	7	(418)	Purych (1973)
Clearwater Bay	6	(560)					Mosindy (1987)
Squeers	7		7-8	(335)	9-11	(415)	Ball (1988)
Robinson	8				12		"
Pettit	6				9		"
Agnes	6				12		"
Pekagoning	12				13		"
Scattergood	5				9		"
Big Shell	8				10		"

variation found in the size of adult females. Relative fecundities vary widely within populations but mean values appear relatively stable across populations about an average of 1597. The lowest mean (1132 for the Iroquois Bay strain of lake trout in South Bay, Lake Huron) is for first-time spawners. More data are needed to determine if spatial variability in relative fecundity is consistently low and also to begin to address the question of temporal variability.

Table 7. Fecundity of lake trout from various Ontario lakes.

Lake	Eggs per female		Eggs per kilogram		Source
	Mean	Range	Mean	Range	
Big Trout		1550-21500	1497		Armstrong (1965)
Opeongo		1500-19074	1609	1129-2059	Martin (1970)
Louisa	996	491-1562	1845	1155-2205	Martin (unpublished)
Sudbury lakes	2674	604-5375	1556	823-2207	Polkinghorne & Gunn (1981)
Squeers	2894	664-19671	1500	1395-1622	Ball (1988)
Manitou	5172	1582-8289	1866	1294-3065	Collins (unpublished)
Georgian Bay	2656	2068-3124			Tomkins (1951)
South Bay[1]	3861	1606-7379	1834	974-2633	Collins (unpublished)
	4774	2998-8263	1132	687-1569	"
Superior[2]	5561	1726-12650	1431		Peck (1988)
Ontario	7943	2452-18051	1589	675-2901	Dymond (1928)

[1] Upper values are for the Lake Manitou strain; lower values for first-time spawners of the Iroquois Bay strain.

[2] Data are from the U.S. portion of the lake.

NATURAL MORTALITY

Reliable estimates of natural mortality (M) are essential for most population models, but not easily obtained. The estimates presented in Table 8 (range 0.11 - 0.26, 5 lakes) represent the few well documented and reliable estimates of natural mortality for Ontario lake trout populations not affected by sea lamprey (*Petromyzon marinus*).

The appearance of a relationship between natural mortality (M) and von Bertalanffy parameters led Pauly (1980) to an analysis of published data for 175 different stocks of fish representing 84 freshwater (including five species of the family Salmonidae) and marine

species from polar to tropical waters. He found that reliable estimates of M were produced by a multiple regression equation:

$$\log_{10}M = -0.0066 - 0.279\log_{10}L_{\infty} + 0.6543\log_{10}K + 0.463\log_{10}T \quad [8]$$

where L_{∞} (total length in cm) and K are the growth parameters and T is the mean annual temperature (^{o}C) of the water in which the stock in question lives. The multiple correlation coefficient was 0.847.

We speculate on the basis of ice free periods, typical lake surface temperatures, and the preferred temperature of the species, that the range of T values for lake trout across Ontario lakes is narrow (5.5-7.5^{o}C). Since a degree change in T alters the estimate of M by only 5%, T can be fixed at 6^{o}C for application of Pauly's equation to lake trout in Ontario without seriously affecting the final outcome. This leaves only two variables in the equation, enabling construction of a table for lake trout (Appendix Table E-1) giving values of M for different combinations of K and L_{∞} (with conversion to fork length).

Available data made estimation of M by the Pauly method possible for three of the lake trout populations in Table 8. The resulting estimates closely resemble those from detailed population studies (Table 8). Given that the three lakes involved range widely in size (384 - 10360 ha), this limited agreement invites further cautious use of the Pauly equation as a quick way of estimating M where representative growth data exist. It might also be used to estimate fishing mortality (F) when total mortality (Z) is known, since F = Z - M. Either use

Table 8. Natural mortality rates (M) from studies of a few Ontario lake trout populations, together with corresponding natural mortality rates determined from growth parameters and temperature by the Pauly method.

Lake	From field studies			By Pauly method
	M	Period	Source	M
Opeongo	0.11	1936-47	Shuter et al. (1987)	
	0.12	1964-83	"	0.12
Squeers	0.22	1982-84	Bail (1988)	0.23
	0.26	1985-86	"	
Manitou	0.22	1958-67	Budd et al. (1968)	0.19
Lake 223	0.14	1976-81	Mills et al. (1987)	
Lake 224	0.23	1976-82	Mills et al. (1987)	

should be with reservation, as the equation is founded on between species, not within species variation.

To gain more insight into the likely range of M over lake trout stocks in the province (exclusive of the Great Lakes), M values were calculated for the 47 lake trout populations in Appendix Table B from their respective K′ and L_∞' values, using Appendix Table E-1. These values for M were normally distributed, with a mean and median of 0.23 and 0.22, respectively, a standard deviation of 0.057, and a range from 0.13 - 0.40. The middle 50% of the distribution occupied the range 0.20 - 0.27. Only one estimate of M exceeded 0.34. The minimum estimate (Lake Opeongo) is slightly above the estimates in Table 8 because of the different estimation procedure for K′ and L_∞'.

OPTIMAL $F_{0.1}$ MANAGEMENT CRITERIA FOR LAKE TROUT

The $F_{0.1}$ management policy or strategy (Gulland and Boerema 1973) is used commonly in marine fisheries but seldom in freshwater fisheries. It is defined as the level of fishing mortality (F) for which the marginal increase in yield-per-recruit resulting from a small increase in F is 10% of the marginal increase in yield-per-recruit that would occur in a lightly

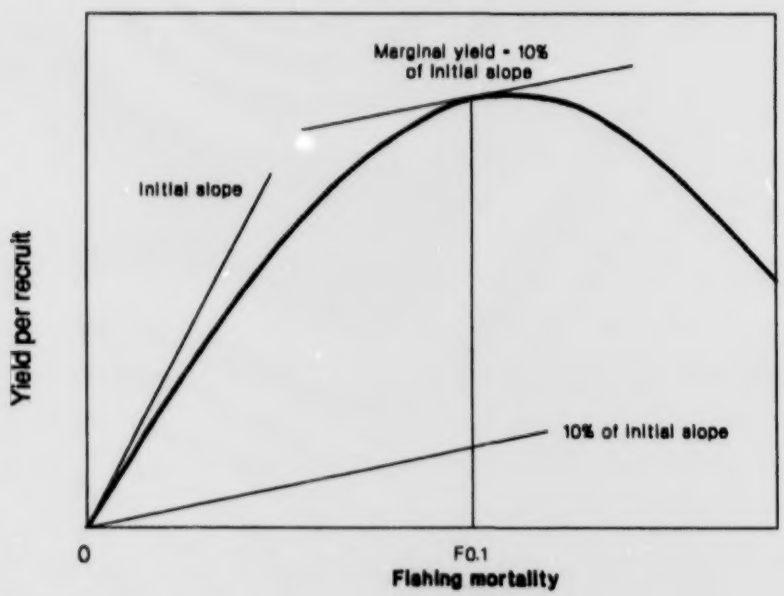

Fig. 7. Determination of $F_{0.1}$ fishing mortality, taken from Deriso (1987).

exploited fishery (Fig. 7). In essence, an $F_{0.1}$ fishing policy returns a yield close to the maximum sustainable yield (MSY), but with greater economy of fishing effort and less attendant risk. Recreational fisheries are not usually managed with economic efficiency in mind and this may explain inattention to the policy in inland areas. However, its amenability to application with simple methods of stock assessment gives the policy an appeal that should not be overlooked.

Associated with the $F_{0.1}$ policy are two control variables, a size of entry of fish into the fishery (L_c) and a specific rate of fishing mortality ($F_{0.1}$). Deriso (1987) defines these as the optimal $F_{0.1}$ criteria and shows how they can be characterized by a single quantity, the ratio of M, the natural mortality rate, to K, the von Bertalanffy growth parameter. Earlier we described how K can be derived from lake trout sample data, even when the determination of age for older fish is a problem. M is less easily obtained by direct estimation but, as we have shown in a prior section, can be approximated using Pauly's (1980) regression equation. Thus, virtually all of the information required to arrive at preliminary estimates of the two control variables can be obtained from lake trout sample data alone.

Pauly's equation, with conversion of L_∞ to fork length and T set to 6°C, has been used to calculate values for M (Appendix Table E-1) and the ratio M/K (Appendix Table E-2) for different paired values of L_∞ and K. Appendix Table E-3 lists the optimal recruitment size (expressed as a proportion of maximum length) for each M/K value, and the instantaneous fishing mortality rate corresponding to M/K and M pairings under an $F_{0.1}$ policy. These were calculated either directly or indirectly using polynomial coefficients supplied by Deriso (1987).

An example will demonstrate how the tables can be used. For Lake Opeongo, Shuter et al. (1987) determined L_∞ and K for lake trout to be 96 cm (88 cm FL) and 0.08, respectively. With this information and Appendix Table E-1, an estimate of M (0.12) is obtained. Similarly, from Appendix Table E-2 a value for M/K (1.51) is derived. In Appendix Table E-3, the optimal size at recruitment for M/K = 1.51 is listed (by interpolation) as 0.58 of the maximum length, which equates to 51 cm FL. The optimal fishing mortality rate (F) for M = 0.12 and M/K = 1.51 is read as 0.13 from the same table. The optimal instantaneous total mortality rate (Z) is the sum of M and F or 0.25. The

corresponding total annual mortality rate (A) of 0.22 may be calculated from the equation $A = 1 - e^{-Z}$ or read from column 3 of Ricker's (1975) Appendix 1.

The question, of course, is whether optimal $F_{0.1}$ criteria developed in this way represent meaningful guidelines for managing lake trout in Ontario. Theoretical support for $F_{0.1}$ criteria founded on M/K is given by Deriso (1987). We address the question empirically, using independently derived results from two well studied lake trout stocks for comparison.

Lake trout in Lake Opeongo (45°52′N, 78°23′W) have been studied continuously since 1936. By regressing Z on fishing effort, Shuter et al. (1987) estimated M from creel survey data for an early (M = 0.11) and a late (M = 0.12) period in the history of the fishery. The estimate from the Pauly equation (M = 0.12) is consistent with these results. An age-structured model of the Lake Opeongo lake trout stock (see page 28) shows sustainable yield maximized at F = 0.16. The optimal $F_{0.1}$ determined from growth parameters alone (0.13) is 19% lower. The optimal size at recruitment from the present analysis (51 cm) has no matching empirical estimate for comparison. It does exceed the current observed size at entry (30 cm, B.J. Shuter, OMNR, Box 5000, Maple, Ont. L0J 1E0, pers. comm.) by a significant margin, but this may be taken as much as a criticism of present fishing practices as a challenge to the validity of the guideline.

Squeers Lake (48°31′N, 90°33′W) was closed to lake trout fishing in 1979, but reopened on an experimental basis in 1985. Survival was estimated from catch curves (1982-1984 gillnet data) to be 0.80 (Ball 1988), leaving annual mortality (A) = 0.20 (equivalent to Z = 0.22). In the absence of fishing, M becomes equal to Z or 0.22. Estimates of survival from catch curve analyses and tag recovery data averaged 0.72 (A = 0.28, Z = 0.33) in 1985-1986, after the onset of fishing. For this later period, M (0.26) can be estimated by subtracting fishing mortality (F = 0.067 from tag returns) from Z (0.33). The current analysis of length-at-age data for lake trout from Squeers Lake (Table 4) indicates that K = 0.17 and L_∞ = 48.5 cm. Using these growth parameters alone and Appendix Table E-1, an estimate of M (0.23) is obtained that falls between the above two empirical estimates. Ball (1988) estimated that Squeers Lake could withstand at least five times the fishing mortality experienced in 1986. Optimal F under an $F_{0.1}$ policy (from Appendix Table E-3 when M = 0.23 and K = 0.17) is 0.26, or 4.0 times the 1986 fishing mortality. The optimal length at

recruitment under $F_{0.1}$ criteria ($0.60 \times L_\infty = 29$ cm) is above the smallest lake trout kept but below the modal size of lake trout harvested (Ball 1988). Thus, in general, guidelines based on an $F_{0.1}$ policy and growth parameters are compatible with management advice based on a detailed study of Squeers Lake.

A summary of the results from detailed population studies and from growth parameters alone follows:

		M	Optimal F	L_c
Opeongo	Detailed study	0.11	0.16	
	Growth parameters	0.12	0.19	51 cm
Squeers	Detailed study	0.22-0.26	0.33	
	Growth parameter	0.23	0.26	29 cm

Optimal F, in this instance, is the value of F meeting the optimization criteria inherent in the analysis, whether they be $F_{0.1}$ criteria or MSY criteria.

The above two sets of comparisons are hardly proof of the relevance of optimal $F_{0.1}$ criteria to Ontario lake trout stocks and of the reliability of the rapid method of estimation. But they do cast the criteria, as derived, in good light. In line with the theory, the $F_{0.1}$ criteria were more conservative than MSY guidelines for the two stocks examined. This built-in conservatism is a desirable feature when regulations must be enacted with a modicum of information and when the species, such as lake trout, is sensitive to exploitation (Olver 1988).

Although simple in application, the foregoing approach to developing management information is by no means simple in terms of the fishery theory on which it is founded. Sceptics should bear this in mind.

ESTIMATING FISHING MORTALITY FOR MAXIMUM SUSTAINABLE YIELDS

Earlier sections of this report have provided empirical descriptions of many aspects of lake trout populations in Ontario. We have shown that lake trout harvest from a population is limited externally by available habitat and that, consequently, potential harvest can be estimated from a quantitative measure of lake trout habitat (e.g. July THV or lake area). We have also established representative values or expressions for length-at-age, weight-at-length, age at first maturity, fecundity and natural mortality - the fundamental relations that shape the internal behaviour of individual lake trout populations. In this section, we provide a method for estimating the level of fishing mortality (F_{msy}) that will provide maximum sustained yield (MSY); we show how the vulnerability of a population to overexploitation can be assessed; and we discuss the influence of recruitment age and young-of-the-year survival on both of these properties of individual populations. These issues are developed in the context of a simple, age-structured population model (Koonce and Shuter 1987).

The model requires the following:

(a) an empirical estimate of MSY (elsewhere stated as potential harvest) derived from a relationship like the one illustrated in Fig. 2;

(b) three values for each age group: weight per individual; fraction of individuals that are sexually mature; and relative catchability of age group members (value for fully catchable ages = 1.0);

(c) a single estimate of fecundity: average number of eggs produced per kg of mature female biomass (=f);

(d) a single natural mortality rate applied to all fish aged ≥1;

(e) a stock-recruit relationship that defines how the number of breeders in the fall of year i determines the number of individuals in year-class i+1 at age 1. We used a Shepherd stock-recruit relation (Shepherd 1982),

$$R = \frac{\alpha f S}{1 + \left(\frac{S}{K}\right)^{\beta}} \qquad [9]$$

where:

R is the number of individuals in a year class at age 1;

S is the total biomass of mature females alive at spawning time;

α is the survival from egg to age 1 when abundance is low enough for density effects to be negligible (in a sense providing a measure of the basic quality of the habitat occupied);

K (units of biomass) controls the influence of adult biomass on egg survival to age 1 (when S reaches K, survival from egg to age 1 is 50% of α);

β adjusts the rate at which early survival declines with increasing values of S (a higher value for β produces a more rapid decline in survival).

In Table 9, we provide a complete list of parameter values for the Lake Opeongo lake trout population. We also provide estimates for 'typical' lake trout populations in small (100 ha), medium (1000 ha) and large (10,000 ha) Ontario lakes. The values for the Lake Opeongo population were derived as part of an extensive analysis of the 48-year time series of data from that stock (Matuszek et al. in press). The values for small, medium and large lake populations were derived mainly from the relations described earlier in this report. Results from the Lake Opeongo analysis were used, where necessary, to fill gaps in data. A more detailed description of parameter estimation procedures follows.

PARAMETER ESTIMATION

MSY for Lake Opeongo was estimated directly using empirical descriptions of the growth, mortality and recruitment characteristics of that population over the period 1960-1975. MSY values for small, medium and large lake populations were estimated from lake area in two steps. First, we estimated THV from lake area using a THV-lake area regression developed from the data in Table 2 (less Lake of the Woods which has only one bay deep enough for lake trout, $r^2 = 0.995$).

$$\log_{10} \text{THV} = 1.186 \log_{10} \text{AREA} - 2.376 \qquad [10]$$

Then we estimated MSY from THV using our THV-sustainable harvest regression equation (equation 1).

The age-specific weight and maturity values for Lake Opeongo are averages for the year-classes 1960-1975. Weight-at-age values for small, medium and large lakes were derived as follows. First, we estimated the von Bertalanffy growth parameters L_∞ and K from lake area, using the regression equations appearing in Fig. 5. Next, we set the von Bertalanffy parameter t_0 to zero (the fitted value for Lake Opeongo) for all lakes. Finally, we used the fully defined von Bertalanffy length equation for each lake to estimate

Table 9. Parameter values for different simulated lake trout populations. Parameter values in parentheses comprise an alternate set.

Parameter	Lake			
	Opeongo	Small	Medium	Large
Area	5560	100	1000	10000
Estimated MSY (kg yr^{-1})	2800	144	975	6590
Natural mortality (yr^{-1})	0.11	0.28	0.23	0.18
Fecundity (eggs kg^{-1} of adult female biomass)	1600	1600	1600	1600
Stock-recruit parameters				
α	0.0035	0.0035	0.0035	0.0035
		(0.0055)	(0.0055)	(0.0055)
β	2	2	2	2
K	4625	7650	5400	15400
		(960)	(2333)	(10282)
Weight at age for ages 1 - 15+	.011,.030	.009,.056	.009,.064	.008,.057
	.053,.134	.148,.272	.177,.341	.170,.339
	.260,.490	.414,.559	.540,.758	.562,.823
	.811,1.14	.698,.826	.981,1.20	1.11,1.40
	1.46,1.80	.940,1.04	1.40,1.60	1.70,1.99
	2.17,2.48	1.12,1.20	1.76,1.91	2.26,2.52
	2.74,2.98	1.26,1.31	2.04,2.16	2.76,2.98
	3.24	1.35	2.26	3.18
Maturity at age for ages 1 - 15+	south:	0,0,0,0,0,.23,.55,.86,1,1,1,1,1,1,1		
	north:	0,0,0,0,0,.1,.3,.5,.71,.91,1,1,1,1,1		
Catchability at age for ages 1 - 15+		0,0,.03,.19,.48,.73,.84,1,1,1,1,1,1,1,1		

length-at-age and then used the average Ontario relation between lake trout weight and length (equation 9) to estimate weight-at-age from length-at-age.

Age specific maturity values were derived for females in typical southern Ontario lake trout populations from the data summarized in Table 6. We assumed that the fraction of mature fish would increase linearly with age and we estimated this relationship by applying regression analysis to the mean ages of first maturity, 50% maturity and 95% maturity, respectively. A similar relationship was derived for northern Ontario populations. We used the southern Ontario values in our comparisons of population behaviour among small, medium and large lakes.

The age specific vulnerability values estimated for the Lake Opeongo population (1960-1983) were used in our simulations for the three lake sizes. This vulnerability schedule is compared to the maturity schedules for southern and northern populations in Fig. 8.

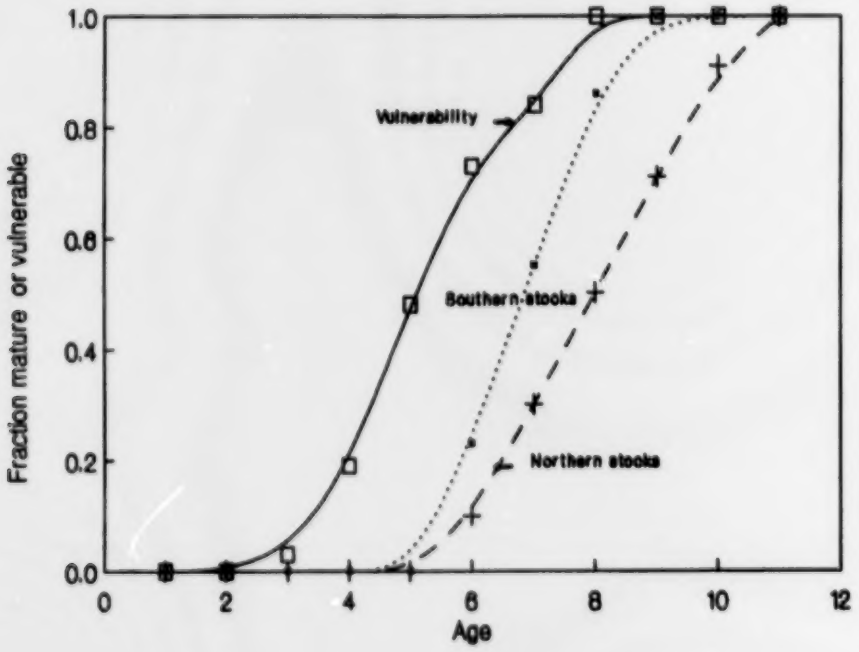

Fig. 8. Age specific maturity curves for female lake trout in southern (....) and northern (----) Ontario populations; age specific values (solid line) for vulnerability to fishing derived from Lake Opeongo data base for the period 1960-1983.

The fecundity estimate for Lake Opeongo (1609) is an average for the entire time series (Martin 1970; Matuszek et al. in press). This value is essentially identical to the average for lakes listed in Table 7 (1597) and is therefore used in all simulations.

The natural mortality rate for Lake Opeongo was estimated directly by regressing annual estimates of total mortality against annual estimates of fishing effort (Ricker 1975). The natural mortality estimates for small, medium and large lakes were derived from L_∞, K and water temperature using the Pauly regression equation (water temperature assumed to be 6^oC for all lakes - see earlier segments of this report for justification). These estimates decline with increasing lake size (Fig. 9).

We used Shepherd's informal procedure for fitting his curve to the stock-recruit data from the Lake Opeongo population. Hence, we estimated α by averaging those values for egg to age 1 survival that fell among the top 10% of values observed over the entire duration of the time series (40 year-classes). And we followed Shepherd's recommendation to assign β a value of 2 for populations where cannibalism occurs (Matuszek et al. in press). Given the above values for α and β, we estimated K from the Opeongo data using non-linear least

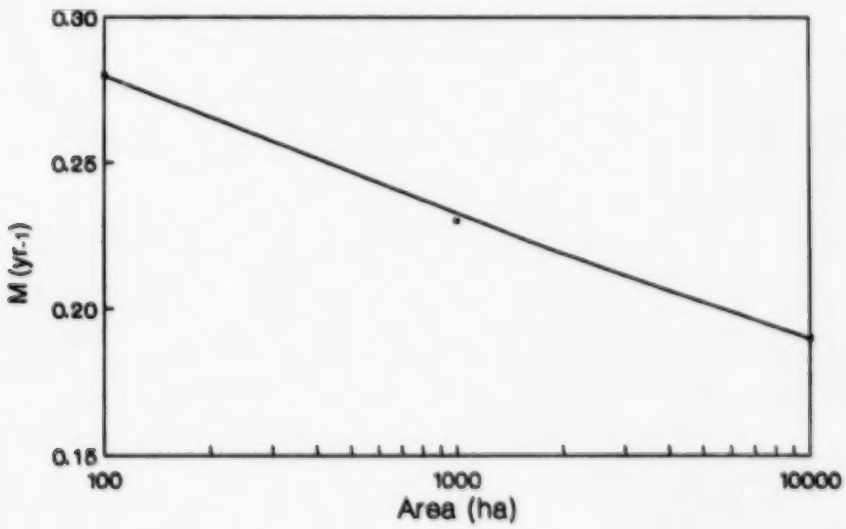

Fig. 9. Relation between natural mortality rate (M) for lake trout aged [illegible]d over and lake area (ha).

squares. Data and fitted curve are shown in Fig. 10. The fit is significant (r2 = 0.36) at the 5% level.

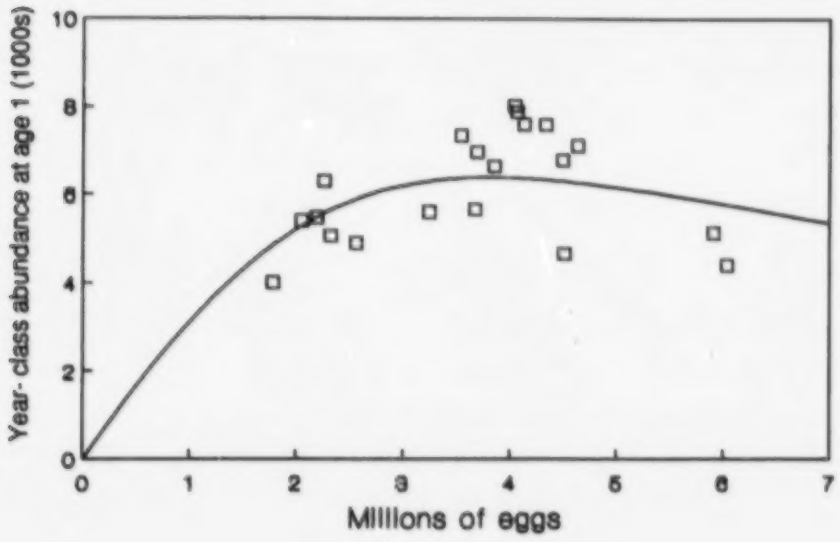

Fig. 10. Relation between year- class strength at age 1 and total number of eggs in mature females for Opeongo lake trout. Data are from year-classes 1956 through 1975. Solid line is a Shepherd stock-recruit relation fitted to these data using methods outlined in the text.

The Opeongo analysis yields a maximum observed value for egg-to-age-1 survival of about 0.0035. Matuszek et al. (in press) showed that extrapolation of these same survival estimates to zero lake trout density yielded a maximum value of about 0.0055. Since Lake Opeongo provides relatively undisturbed, high quality lake trout habitat, we argue that these two values establish a reasonable range for this parameter for most Ontario lakes containing good lake trout habitat. Given the absence of additional information, we used this 'Lake Opeongo' range for α and a value of 2 for β in our simulations of the behaviour of lake trout in small, medium and large lakes.

We used our area-based estimates of MSY (Table 9) to derive individual K values for lakes of different size. Fig. 11 shows that the value for MSY calculated from our Lake Opeongo population model is essentially proportional to K, while the value for F_{msy} is relatively independent of K. We derived similar MSY vs K from our models of small,

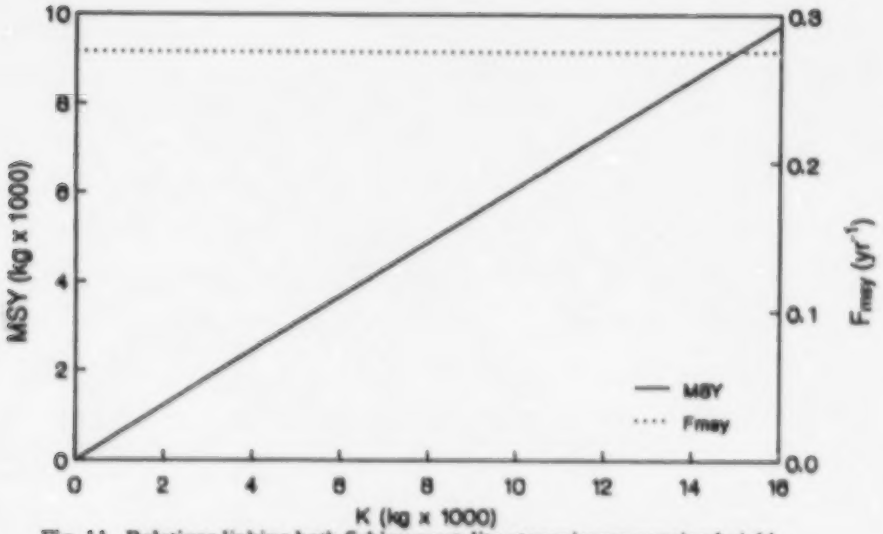

Fig. 11. Relations linking both fishing mortality at maximum sustained yield (Fmsy) and maximum sustained yield (MSY) to the parameter K of the Shepherd stock-recruit relationship. Each relation was generated using the age-structured population model described in the text and parameterized for the Lake Opeongo lake trout population.

medium and large lake populations and used them to estimate lake-specific values for *K* that would match our empirical, area-based MSY estimates. In this way we obtained a quantitative description of the the relation between *K* and lake area (Fig. 12). Although in reality *K* will fall below the pristine lake trout biomass, it can be likened to carrying capacity in

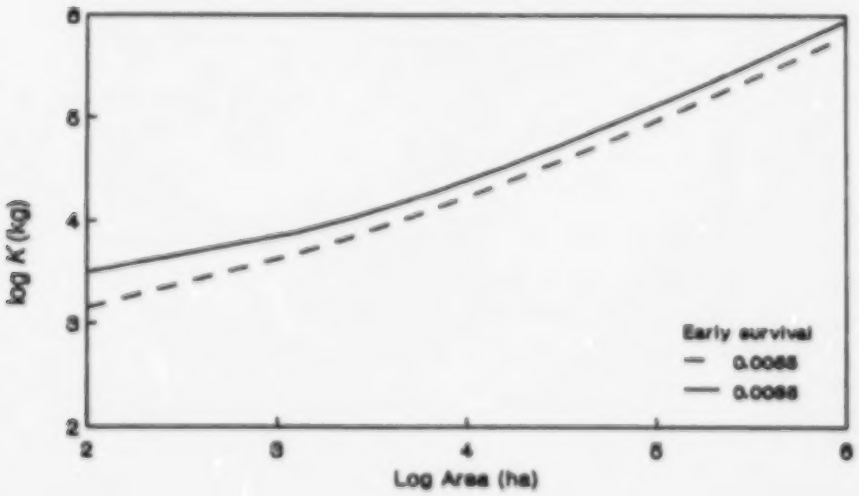

Fig. 12. Relation between the Shepherd stock-recruit parameter K and lake area. The solid curve was derived assuming a value of 0.0035 for maximum early survival; the dashed line was derived assuming a value of 0.0055. A maturity curve characteristic of southern Ontario lake trout populations was used in all calculations.

that its effect on population regeneration is similar. Therefore, we have in Fig. 12 an explicit description of how population carrying capacity may increase with increases in lake size.

POPULATION SIMULATION

All of the lake populations listed in Table 9 share the following two characteristics: a domed-shaped stock recruitment relationship and a low natural mortality rate for older fish. Because of these shared characteristics, all will exhibit the following properties to some degree: unexploited populations will have a bi-modal size structure (Fig. 13); and as fishing mortality increases, equilibrium values for recruitment will increase gradually, peak, and then decline rapidly (Fig. 14).

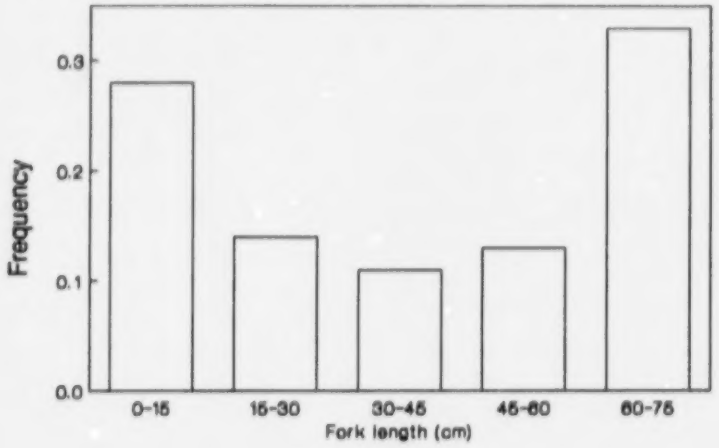

Fig. 13. Predicted size distribution for the Lake Opeongo lake trout population assuming no exploitation. These data were generated by the age-structured model parameterized for the Lake Opeongo lake trout population.

Sustainable yield (SY) curves for the small, medium and large lake populations are illustrated in Fig. 15 and summarized in Table 10 and Fig. 16. These results indicate that:

(a) SY curves are asymetric (as F increases, SY rises slowly and then declines rapidly) (Fig. 15) as a consequence of the asymetry inherent in the performance (Fig. 14) of the stock-recruit function used;

(b) F_{msy} increases with lake size (Fig. 16);

(c) F_{ext} (the level of fishing mortality just sufficient to drive the population to extinction) increases with lake size (Table 10);

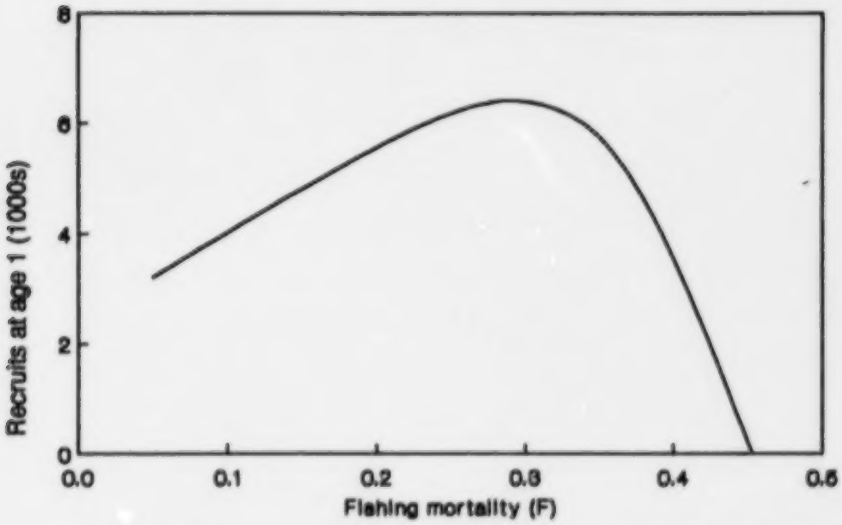

Fig. 14. Relation between average year-class strength at age 1 and fishing mortality rate (F). These data were generated by the age-structured population model parameterized for the Lake Opeongo lake trout population.

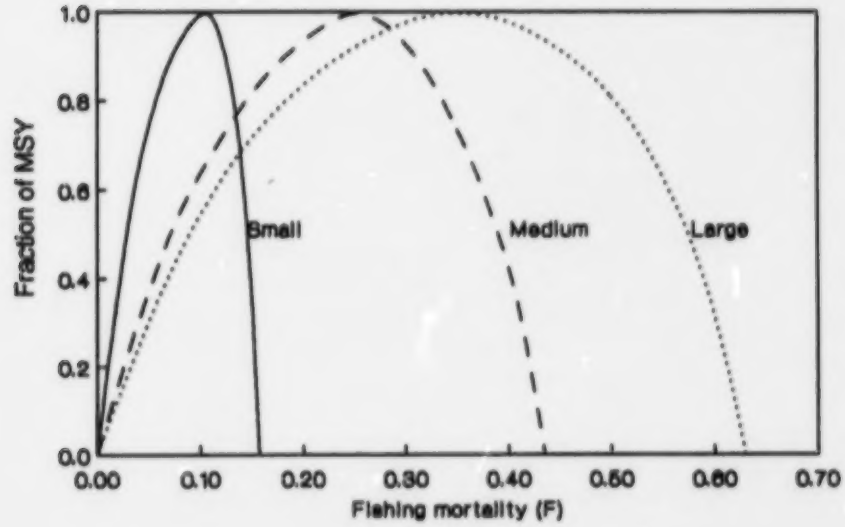

Fig. 15. Relations between sustained yield (SY) and fishing mortality (F) for small, medium and large lakes. Each curve was generated using the age-structured population model parameterized for the size of lake according to the values listed in Table 9 of the text. A maturity curve characteristic of southern Ontario populations was used in all calculations. The SY values for each curve have been divided through by the maximum sustained yield for that curve.

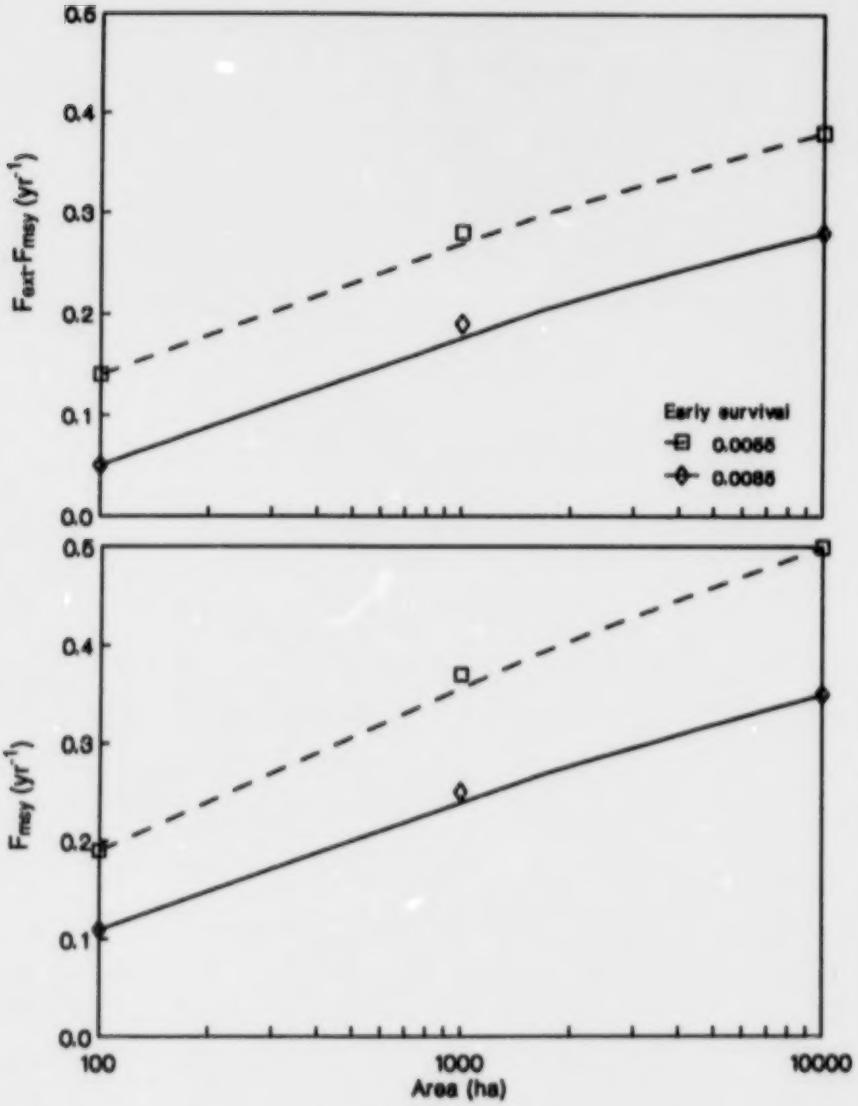

Fig. 16. Relations linking lake area to: fishing mortality at maximum sustained yield (F_{msy}) (lower panel); the difference between F_{ext} (fishing mortality just sufficient to eliminate the population) and F_{msy} (upper panel). These data were generated by the age-structured population model parameterized for the size of lake according to the values listed in Table 9 of the text. A maturity curve typical of southern Ontario lake trout populations was used in all calculations. The solid line gives results for early survival at 0.0035; the dashed line for early survival at 0.0055.

Table 10. Summary of results from simulations of various lake trout populations. The smaller figure in each cell was derived with maximum first year survival set to 0.0035; a value of 0.0055 was used to derive the larger, bracketed figure.

Statistic	Lake Opeongo	Small lake	Mid-size lake	Large lake
F_{msy}	.28 (.40)	.11 (.19)	.25 (.37)	.35 (.50)
F_{ext}	.45 (.66)	.16 (.33)	.44 (.65)	.63 (.88)
F_{ext}-F_{msy}	.17 (.26)	.05 (.14)	.19 (.28)	.28 (.38)
M	.11	.27	.23	.18
Z_{msy}	.39 (51)	.38 (.46)	.48 (.60)	.53 (.68)
Z_{ext}	.56 (.77)	.43 (.60)	.67 (.88)	.81 (1.06)
A_{msy}	.32 (.40)	.32 (.37)	.38 (.45)	.41 (.49)

(d) sustainable yields of small lake populations are more sensitive to changes in F; the difference between F_{ext} and F_{msy} increases rapidly with increasing lake size (Fig. 16), reflecting the fact that the SY curve for small lakes is narrower around MSY than is the SY curve for large lakes (Fig. 15).

These trends with respect to lake size stem directly from the negative relationship between lake size and natural mortality (Fig. 9).

Fig. 16 illustrates how the essence of SY vs F curves (Fig. 15) can be captured in terms of two summary statistics: F_{msy}, the level of fishing mortality required to obtain MSY; and the difference between F_{ext} and F_{msy}. The difference between F_{ext} and F_{msy} provides a useful measure of the vulnerability of a population to overexploitation. If this difference is small, exploitation levels only slightly greater than that required to provide MSY will produce catastrophic declines in population abundance. If this difference is large, acceptable abundance levels can be maintained over a wide range of exploitation levels around that required to produce MSY.

The results in Table 10 illustrate the sensitivity of F_{msy} and F_{ext}-F_{msy} to changes in natural mortality and the inverse nature of the relationships. Both quantities are equally sensitive to changes in any of the other population parameters that directly affect the rates at which new individuals join the breeding segment of the population or old individuals leave it. Both F_{msy} and F_{ext}-F_{msy} increase with increases in either early survival (Fig. 17) or weight-specific fecundity. Similarly, both F_{msy} and F_{ext}-F_{msy} increase with increases in the age of recruitment to the fishery (Fig. 18). This last relationship is of particular interest

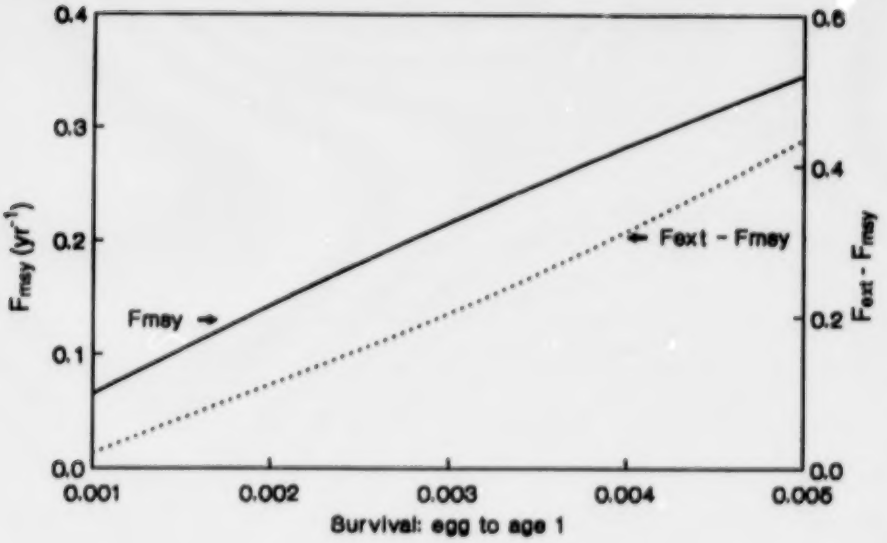

Fig. 17. Relations between egg-to-age-1 survival and: F_{msy}; the difference between F_{ext} and F_{msy}. These data were generated by the age structured population model parameterized for a medium sized lake, according to the values listed in Table 9.

since age of recruitment can be manipulated by managers. The behaviour illustrated in Fig. 18 is summarized below:

(a) when age of recruitment to the fishery is (age of maturity - 2 years), F_{msy} remains close to 0.2; F_{msy} increases rapidly as age of recruitment approaches age of maturity;

(b) sensitivity to overexploitation declines with increases in F_{msy}, while MSY itself is not greatly affected.

(c) if the lake trout populations of northern Ontario must withstand the same exploitation levels as southern populations,then a later recruitment age is required to compensate for the later age of maturity characteristic of northern populations.

The results summarized in Table 10 and Figs. 15-18 show that, over a wide range of values for fecundity, early survival and natural mortality, F_{msy} lies mainly in the range 0.1 to 0.4 yr^{-1}. Only when immature fish are systematically excluded from the fishery are higher values observed. With natural mortality (M) itself roughly in the range from 0.1 to 0.3, it follows that populations experiencing total instantaneous adult mortalities (Z) in excess of 0.7 yr^{-1} are almost certainly overexploited, while populations experiencing rates in the range

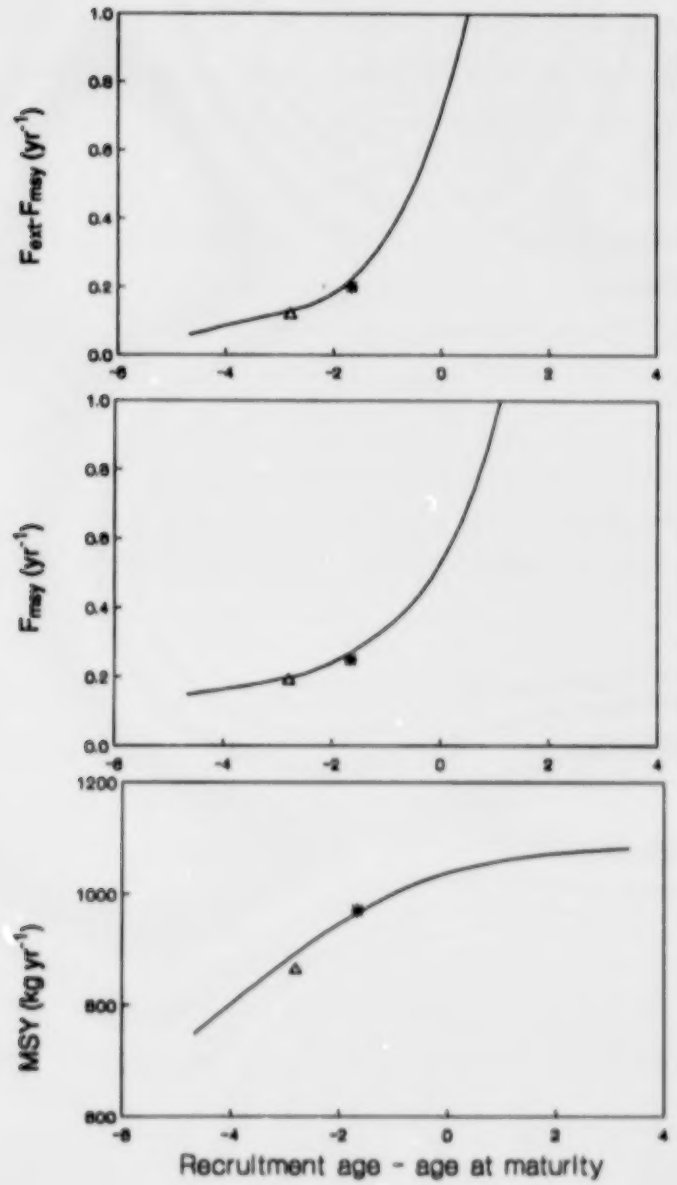

Fig. 18. Relations linking the quantity (mean age of recruitment to the fishery - mean age of first maturity) to maximum sustained yield (MSY), fishing mortality at MSY (F_{msy}) and the difference between F_{ext} and F_{msy}. These data were generated by the age structured population model parameterized for a medium sized lake, according to the values listed in Table 9. The solid curve gives results obtained by changing the age of recruitment to the fishery while keeping age of maturity constant at a value typical for southern Ontario; • marks values obtained with the Table 9 vulnerability schedule and a southern Ontario maturity schedule; Δ marks values obtained with a Table 9 vulnerability schedule and a northern Ontario maturity schedule.

0.6 to 0.7 may be. This range becomes 0.45 to 0.50 when expressed as total annual mortality (A). This finding suggests that the past informal guideline that annual adult lake trout survival be maintained above 50% has not been too conservative; in instances it may have been too liberal.

In summary, we have shown that a simple, age-structured population model can be used to integrate our knowledge of habitat limits on population production with our knowledge of the internal relations that govern population behaviour in a way that permits us to estimate F_{msy}. We have also shown that a very rough estimate of the F_{msy} for a lake trout stock can be obtained from lake area alone. This estimate can be refined if additional biological information (e.g. size-at-age, age of maturity, adult natural mortality) and fishery information (age of recruitment to fishery) are available. The accuracy of the method hinges on information gained from intensive field studies of a small number of typical stocks (e.g. Lake Opeongo).

Use of the model need not be confined to these applications. Indeed, its greater value may be as a tool for heuristically exploring the consequences of alternate management actions and the attendant areas of uncertainty and risk.

DISCUSSION

Potential harvests (kg yr^{-1}) estimated from the THV model for lake trout will be proportionately greater for small lakes than for large lakes. Otherwise stated, greater yields (kg ha^{-1} yr^{-1}) are projected for smaller lakes. This aspect of the model follows directly from the data in Table 2 which exhibit an inverse relationship between lake area and yield. Such a relationship likewise was observed by Goddard et al. (1987) and Carl et al. (1990) for Ontario lake trout lakes alone. Lower species diversity in smaller lakes (Carl et al. 1990) may account for this, in part, by lessening the number of species in competition with lake trout. There is also the argument, challenged by Kerr and Martin (1970), that the shorter food-chains generally associated with the simpler fish communities of small lakes reduces the total energy loss occurring between trophic levels. An explanation, perhaps related, can also be found among lake trout population parameters. The higher von Bertalanffy K values

and natural mortality rates which appear to characterize lake trout populations in small lakes also signify higher turnover rates, and turnover rate typically dictates the potential for yield.

The wide prediction limits about estimates of potential harvest for individual lakes from the THV model (Fig. 2) may be unsettling, but all signs indicate that this model for lake trout is still preferable to the current alternative - a partitioning of the MEI yield estimate for all species. The question as to which of the two methods would be more reliable is one which we have addressed in several ways. For the 20 lakes in Table 2, potential yields were estimated by both the THV method and the partitioning method (lake trout yield = $0.25(1.38\ MEI^{0.446})$ OMNR 1982). For 12 of the 20 lakes, the THV method produced the more conservative estimate. For the five Ontario lakes which had been added, the THV estimates were the higher. However, for Bone and Christman lakes the THV estimates were still below the actual harvest; for Opeongo Lake the THV estimate was almost identical to the actual harvest; and for Flack Lake lake the THV estimate was only 1.2 times the actual harvest. A THV estimate 1.7 times the actual harvest occurred with Chiblow/Denman Lake, but along with Lake Opeongo this lake had quite low fishing intensity (3.2 ang-h ha^{-1}) and may not have been fished at potential. Overall fit by the two methods was examined by regressing the (log) actual harvest on the (log) estimated potential harvest for each of the estimation procedures. The resultant r^2 values were 0.97 and 0.88 for the THV and partitioning methods, respectively, showing the THV method to be the better fitting of the two.

The latter comparison is, however, not entirely fair; the THV model was developed empirically from the same set of lakes, whereas the partitioning method employs a "universal" MEI equation. To allow the MEI approach to be viewed under more similar light, we used log transformed data from our 20 lake data set (Table 2) for an empirical examination of the relationship between MEI and lake trout yield. Little relationship was actually found to exist ($r^2 = 0.076$). Obviously, the r^2 above for the partitioning method is as high as it is (0.88) because of the area multiplier. In fact, as shown below, lake area and lake volume both are better predictors of lake trout harvest than a partitioned MEI

$$\log HARVEST = 0.500 + 0.830 \log AREA \qquad r^2 = 0.923 \qquad [11]$$

$$\log HARVEST = 1.596 + 0.695 \log VOLUME \qquad r^2 = 0.934 \qquad [12]$$

Confidence limits for the MEI estimator for yield, even after reformulation to avoid artificial correlation, separate by a factor of five (Schneider and Haedrich 1989), vs an order of magnitude for THV. And this is before the uncertainty of partitioning is introduced. Thus, you could only expect the partitioning approach to be an improvement over THV if the fraction of total yield comprised of lake trout is both a conservative property of lake trout lakes and precisely known. It seems safe to say that neither of these conditions is met. Given this and the foregoing considerations, we would not recommend the MEI partitioning method for estimating potential harvest for lake trout when other methods are available.

Shuter and Regier (1989) point to the difficulty of assessing and expressing habitat loss in terms relevant to a public that tends to focus primarily on fish species of high value. Quantitative measures of habitat that afford a basis for predicting sustainable harvest for a species are useful in this context because they also enable some forms of habitat deterioration to be expressed in terms of reduced harvest. The THV model falls clearly in this category, which is another reason for favouring it over other potential harvest predictors. In the instance where low oxygen excludes lake trout from some part of its THV (see page 9), the loss in usable THV directly influences the harvest expectation.

Growth in lake trout is density dependent, hence the proposition that growth differences within and between stocks may shed light on differences in numeric stock status (OMNR 1983). We stress the word "may" because there are other circumstances which affect growth. Extremely rapid growth usually does signify lower than optimal lake trout densities. Interpretation of slow growth is less certain as diet, competition, and the physiological demands of the environment all can impose limitations. Slow growth in association with low density may be symptomatic of some added stress and should be viewed by managers as an abnormal condition deserving attention. For example, in one experiment, lake acidification was found to depress lake trout abundance and growth, although at a later stage than expected (Mills et al. 1987).

Condition (weight relative to length) is a more sensitive indicator of change in relative food supply and hence of lake trout density change, than length-at-age, as a consequence of the lower ordering of somatic growth in the allocation of ingested nutrients (J. Casselman, OMNR, pers. comm.). This is demonstrated by lake acidification studies where change in

lake trout condition was noted soon after initial lake treatment and well before any growth rate change (Mills et al. 1987). This indicator also has the advantage of involving measurements (length and weight) which can be precisely taken. Even more precision can be achieved in comparisons of condition if variability attributable to gonad development and food ingestion is eliminated by subtracting those portions of the body weight, provided all data conform to this treatment.

There are various indices of condition from which to choose, each having one or more critical assumptions (Cone 1989). With the more commonly used Fulton condition factor (Ricker 1975), the assumption is that growth is isometric ($b \cong 3.0$). Values of b given in Table 5 indicate that this assumption does not hold for lake trout populations in Ontario. Likewise, the assumption of constant b inherent in the relative condition factor (Le Cren 1951) would appear invalid for Ontario lake trout, based on our observations (Table 5). Relative weight, the ratio of an individual's weight to a "standard" weight (Wege and Anderson 1978), is even more demanding in its assumptions, requiring the slope (b) and intercept (a) of the weight-length regression to be the same as that for some defined "standard" population. Our values of a and b for lake trout, contrary to this, are quite variable. Cone (1989) has recommended that condition indices, because of their limitations, be replaced with estimates of least-squares regression parameters. For lake trout, at least, we tend to agree. If condition factors are used, they are perhaps best used to detect change within populations.

Growth differences observed among lake trout stocks in Ontario have been largely ignored when considering how lake trout fisheries should be regulated. Our applications of growth data in connection with $F_{0.1}$ criteria and also as a variable in separate trials with the age-structured model reveal, in convincing fashion, the importance of this aspect of lake trout dynamics.

We have described two methods of calculating a rate of fishing mortality consistent with a high sustainable yield. Both methods can be employed by managers with a modest amount of readily obtainable data, although it is clear that the utility of the age-structured model in dealing with a particular lake will be much enhanced if parameter estimates specific to that lake are available. There are important differences between the two methods. The

$F_{0.1}$ criteria are, by definition, more conservative (but see later discussion); Deriso's Fig. 4, coupled with our observation that the M/K ratio for lake trout ranges from approximately 1.0 to 1.5, suggests that fishing in accordance with $F_{0.1}$ criteria would return 83% of the maximum sustainable yield. The $F_{0.1}$ criteria represent simultaneous optimization for both size at entry and fishing mortality rate (provided, of course, that the rationale underlying $F_{0.1}$ fishing is considered a suitable basis for optimization). Optimization with the age-structured model must be confined to one variable at a time, with other mutually related variables held constant. The advantage of the age-structured model is that it does allow for dependence of recruitment on stock size. It also recognizes differences in the maturation schedule. Of significance and not previously stated, the derivation of optimal $F_{0.1}$ criteria represents an extension of basic yield-per-recruit theory and therefore fails to recognize any relationship between stock size and recruitment.

The characterization of optimal $F_{0.1}$ criteria by the ratio of M/K alone is a weakness which varies in its consequence according to the value determined for the parameter α in the Ricker stock-recruit relationship (assuming that this formulation applies) (Deriso 1987). Providing the biomass of recruits (at length Lc) remains greater than 1.5 times the product of the fishable biomass at equilibrium and the natural mortality rate (M), the $F_{0.1}$ criteria should not place unreasonable demands on the spawning stock (see Deriso's Fig. 5). The important point to remember concerning these optimal criteria (Lc and $F_{0.1}$) is that they are mutually dependent and intended to be applied as a set of controls.

The sensitivity of lake trout to exploitation (Olver 1988) can be readily explained if the model results relating recruitment and sustainable yield to fishing mortality hold for lake trout populations in general. Recruitment declines abruptly beyond some threshold value of fishing mortality (Fig. 14) that appears at or very nearly at Fmsy. Sustainable yield curves (Fig. 15) show corresponding sharp declines close to Fmsy. The figures describe ultimate steady states achieved from a largely deterministic model; stochasticity would add to the risk near the 'breaking point'. It can reasonably be assumed, as well, that lake trout populations undergoing rehabilitation will not be well served by the higher fishing mortality rates suggested by this analysis. Such populations require special protection, especially if other species have encroached on the lake trout niche. Conservative allowances for fishing in such circumstances should be the rule.

The simulations of lake trout populations in small (100 ha), medium (1000 ha) and large (10,000 ha) lakes show smaller lakes with a lower rate of fishing mortality at MSY and with yields that are highly sensitive to changes in fishing mortality (Fig. 15). Both attributes place smaller lake trout lakes at greater risk of overexploitation. It is important to remember that these results are greatly influenced by relationships between lake size and lake trout growth and mortality which are only weakly demonstrated. Hence, there will be exceptions. More longterm and in depth studies of the Lake Opeongo type are needed to reinforce and expand this aspect of our understanding of lake trout dynamics and to gain greater lake-size representation.

It is also important to remember that somewhat different results are obtained from an $F_{0.1}$ analysis of lake size effects. Using the empirical relationships between the two growth parameters and lake area (Fig. 5), separate L_∞ and K values can be calculated for lakes of the three sizes used in our earlier comparison (100, 1,000 and 10,000 ha). These values when used as entries into Appendix Tables E-1 to E-3, give three different values for optimal $F_{0.1}$ which decrease linearly with log of lake size from 0.35 to 0.23; the suggestion being that lakes of smaller size can withstand higher safe levels of mortality from fishing. Two explanations for this apparent contradiction in results can be offered. Size (actually age) at entry in the age-structured model was fixed whereas in the $F_{0.1}$ analysis this value is returned as an object of the optimization process. Thus, the fishing regimes differ. The second and major difference between the two analyses relates to accommodation of stock size effects on the replenishment of the fishery. The stock-recruit function built into the age-structured model enables stock replacement needs as well as natural mortality and growth to be weighed in determining an optimal F. The $F_{0.1}$ approach takes into account only natural mortality and growth. The contrasting result suggests that the stock-recruit relationship may remain important even at lake trout densities generally associated with a productive stock. Given that the age-structured model encompasses more elements of the dynamics of lake trout populations, we attach more credence to its general, if not specific, representation of varying fishing mortality rates with lake size. At the same time, we find heartening the fact that the $F_{0.1}$ analysis gives estimates for optimal F which lie in roughly the same range as the two estimates returned by the age-structured model for a mid-sized lake (0.25-0.37, Table 10).

Population simulation has indicated that the optimal rate of fishing mortality increases and becomes less sharply defined as the age (size) of recruitment increases relative to the age at maturity (Fig. 18). Delaying the age at recruitment by imposing a minimum size limit therefore makes sense, especially in high fishing demand areas where fishing effort is difficult to limit by indirect means such as seasons, but only if hooking mortality among released undersize fish is low enough. A slot limit might achieve the same effect and allow anglers to catch more, if not larger, fish. Both forms of harvest control are amenable to exploration using the age-structured model. Given the sensitivity of lake trout to overexploitation, both should receive serious consideration by managers.

Lake trout catchability, or the efficiency with which individual units of fishing effort catch lake trout, is important in both modelling and management contexts. Increases in lake trout catchability brought about by changes in angling technology will cause fishing mortality to increase without fishing effort seeming to change. But the ramifications of such technological change can be even greater if there is direct dependency of fishing effort on fishing success, and there is some evidence that this is the case. Goddard et al. (1987) observed that for 32 lake trout lakes where catch and effort values for two consecutive years were available, the change in effort from year 1 to 2 was significantly ($p < 0.01$) correlated with catch-per-unit effort in year 1. Enhanced catchability can make the fishery appear better when no real change in the stock has taken place and, when this happens, more angling effort is likely to be attracted into the fishery. The effects of technological change can thereby be compounded. With or without compounding, the effects of technological change in angling fisheries must not be ignored. If allowed in lakes which are already intensively fished, some form of compensation will be necessary. Otherwise, in the longterm, overfishing will occur and both the resource and angling quality will suffer. For overfished stocks, the trend toward improving angler efficiency might have to be legislatively reversed, at least during the period of recovery. Even with fishery restrictions, rehabilitation can be a long-term proposition (Evans et al. 1990).

MANAGEMENT IMPLICATIONS

Managers of lake trout in Ontario have been handicapped by lack of a direct means of estimating the potential of individual lakes for lake trout production; lack of a reliable set of diagnostics that would allow the state of a lake trout population to be evaluated; and lack of analytical tools for determining the level of fishing that might best protect a lake trout population and yet allow realization of its potential. These shortfalls have combined to leave managers uncertain in some instances about the need for regulatory change; in a quandary in other instances over the type of change to make; and almost always ill-prepared to argue convincingly of the need for change. This paper offers some relief in these areas.

Our reformulation of Christie and Regier's (1988) estimator of sustainable harvest now gives managers a specific and practical means of estimating the potential harvest of lake trout from lakes and secondarily a means of expressing certain types of habitat loss in terms of reduced potential harvest. Although seemingly a better estimator of potential lake trout harvest, this model still does not offer high precision. Use of the model should therefore be tempered with discretion and with the thought in mind that the relationship which it describes is derived from a set of lakes generally considered to be among the better lake trout lakes. Marginal lake trout lakes can not be expected to produce to the same standard.

Analyses of growth in lake trout in the past have been confounded by bias in age determinations. We offer a temporary solution which permits the fitting of a growth curve using only age-length data from lake trout that are young and length data from lake trout that are large. Use of the method should lead to better interpretations of past growth data and allow reduced sample sizes in any future growth studies where high resolution is not needed.

Representations of lake trout growth (length-at-age and weight-at-length) given in this paper show the distribution of growth parameters for Ontario lake trout populations and also the central tendencies. Median conditions for both forms of growth expression are offered as new or updated standards for comparison when applying a diagnostic approach to stress analysis (OMNR 1983). We reiterate that such use presupposes strong dependency of growth on lake trout density. While differences in lake trout growth through time and within a lake

are likely to be density related, point in time differences in growth between lakes are apt to be founded on differences in the respective biotic or abiotic environments. This is a cautionary statement calling for good sense when using growth as a measure of stress.

What does emerge from this paper is greater recognition of the importance of growth in lake trout dynamics, an importance which is due, in part, to an apparent connection between growth parameters and the rate of natural mortality. The implication is that considerable information about the dynamics of a particular lake trout population can be gleaned from growth data alone and procedures are given for making this connection. These procedures call upon the work of Pauly (1980) for the estimation of natural mortality from von Bertalanffy growth parameters and the work of Deriso (1987) for the estimation of the optimal rate of fishing and recruitment size from the natural mortality rate and von Bertalanffy's K parameter. Our limited but favourable experience using growth data in this way makes credible the concept of using a few, easily measured, key parameters to gain deeper insights into the character and productivity of fish populations.

Compilations of maturity and fecundity data that we present need future expansion but nevertheless are informative. Relative fecundity would appear to vary little across lake trout populations and most populations should be quite well represented by a value of 1600 eggs kg^{-1} of adult female biomass. In contrast, maturity schedules are quite variable with at least some of the variability apparently related to latitude. It follows that time to maturity should be addressed in future studies.

The lake trout has a comparatively low reproductive potential and, therfore, depends heavily on its considerable longevity and capacity for multiple spawnings for population maintenance. One might expect on this basis that the size of the adult population would have considerable bearing on the productivity of a lake trout population. Our modelling of lake trout populations tends to bear this out. In simulations, recruitment and, consequently, sustainable harvests of lake trout are negatively impacted at total mortality rates below those routinely reported for Ontario lakes. Total mortality rates (A) in excess of 0.45 - 0.50 might, in fact, be regarded as one measure of overexploitation, although this may vary with lake size (Table 10). Judging from these results, fishing must be a leading cause, if not the leading

cause, of distress among lake trout populations in inland waters. Lake trout populations that are depressed are unlikely to fare well until fishing is brought more under control.

Managers would appear to have three options for holding exploitation within acceptable bounds:

(1) altering the way in which anglers fish to reduce the efficiency with which they catch some or all size classes of lake trout;

(2) reducing fishing effort through some combination of seasons and creel limits;

(3) restricting the age range over which lake trout may be kept by imposing a minimum size limit or slot limit.

The first option goes counter to a trend toward "high-tech" fishing methods, especially for deep-dwelling coldwater species, but may have appeal in some situations, for example where there is interest in maintaining a wilderness experience. Restricting fishing effort may satisfy the needs of lake trout, but leaves managers in the unenviable position of further reducing fishing opportunities each time demand increases. Restricting the fraction of the population from which "keepers" may be drawn becomes a plausible solution because it allows angling to continue and eventually offers the benefit of higher catch rates, if not retention rates. With this latter option, hooking mortality comes into the equation and may eventually undermine the approach unless anglers can be convinced to limit their catch as well as their kill of lake trout. Public education will be a necessary part of any solution because, without public understanding and support, no corrective measure is likely to succeed.

Relationships between lake size and rates of growth and natural mortality have important implications for lake trout management as their net effect is to place smaller lake trout lakes at greater risk of overexploitation. It is important, here, not to confuse fishing mortality rate and yield. It has been established empirically that small lake trout lakes, on average, will sustain higher yields. The risk mentioned above stems from the fact that, with small lake trout lakes, a comparatively low level of fishing mortality is sufficient for realization of that yield. In addition, lake trout in small lake trout lakes, would appear relatively intolerant of fishing in excess of that low level. The combination of high yield and low

fishing mortality rate is made possible by a high biomass of small fish in small lakes (Carl et al. 1990). The conclusion is that there is no single fishing regime which is optimal for all lake trout lake lakes.

Most lake trout lakes in Ontario are aggregated in fishing divisions for the purpose of fishery regulation. This raises questions concerning ways to meaningfully apply lake-specific management guidelines such as those produced by an $F_{0.1}$ optimization analysis. One way is to use those guidelines as a basis for arriving at sets of lakes which have common requirements for control of fishing. This might logically be done on a regional basis. Ultimately, the objective should be to have management zones for lake trout wherein the various lake trout populations have similar dynamics and perhaps other matching qualities.

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APPENDICES

Appendix A. Sample calculations for thermal habitat volume (THV).

The following data are required to calculate THV:

- at least one temperature-at-depth profile from July
- an area-at-depth profile
- maximum depth

Note that these should be available from lake inventory data.

The first step in calculating THV involves combining individual mid-summer temperature profiles into a single "average" profile for the lake. Below, we use Christman Lake as an example. Two profiles were available for this lake:

Profile 1 (67.June.17 lake survey)		Profile 2 (75.Aug.13 Hydrolab)	
Depth (m)	Temperature ^{o}C	Depth (m)	Temperature ^{o}C
0.0	17.8	0.7	22.6
1.5	17.2	3.0	22.6
3.1	15.6	5.7	11.6
4.6	13.3	7.7	7.2
6.1	8.3	9.9	6.1
7.6	7.2	12.3	5.3
9.1	6.7	15.4	4.9
10.7	6.1		
12.2	6.1		
13.7	5.6		
15.2	5.0		
16.8	5.0		
18.3	5.0		

These profiles were interpolated linearly for 2.5 m depth intervals from the surface to the maximum depth (18.3 m for Christman Lake). If no reading was available at the surface, the surface temperature was set to the shallowest reading. If the profile did not extend to the maximum depth, a temperature of 3^{o}C was assumed for that depth. The basic formula

used for interpolation was:

$$T_I = T_1 + \frac{(D_I - D_1)(T_2 - T_1)}{(D_2 - D_1)} \quad \text{where}$$

T_I = the interpolated temperature for a given 2.5 m depth interval

D_I = a given 2.5 m depth interval

T_1 = the temperature from the closest actual reading with depth < the current 2.5 m depth interval

T_2 = the temperature from the closest actual reading with depth >= the current 2.5 m depth interval

D_1 = the depth where T_1 was taken

D_2 = the depth where T_2 was taken

This gave the following profiles:

Profile 1		Profile 2	
Depth (m)	Temperature (^{o}C)	Depth (m)	Temperature (^{o}C)
0.0	17.8	0.0	22.6
2.5	16.2	2.5	22.6
5.0	12.0	5.0	14.5
7.5	7.3	7.5	7.6
10.0	6.4	10.0	6.1
12.5	6.0	12.5	5.3
15.0	5.1	15.0	5.0
17.5	5.0	17.5	3.5

The individual interpolated profiles were than averaged at each depth to get a single profile:

Depth (m)	Temperature (^{o}C
0.0	20.2
2.5	19.4
5.0	13.2
7.5	7.5
10.0	6.2
12.5	5.6
15.0	5.0
17.5	4.2

The same procedure is used to generate an interpolated depth-at-area profile:

Raw profile		Interpolated profile	
Depth (m)	Area (ha)	Depth (m)	Area (ha)
0.0	58.6	0.0	58.6
3.1	42.3	2.5	45.5
6.1	30.2	5.0	34.6
9.1	16.1	7.5	23.6
12.2	10.6	10.0	14.5
15.2	6.2	12.5	10.2
18.3	1.5	17.5	2.7

The depths at which 12 and 8°C occur are interpolated from the final temperature profile. These were 5.52 and 7.26 m, respectively. Corresponding areas for these depths were interpolated as 32.32 and 24.65 ha. The volume of water in hm^3 for this "slice" was calculated from the formula

$$V = \frac{(D_2 - D_1)}{300\,(A_1 + A_2 + \sqrt{(A_1 \times A_2)}}$$

where D refers to depth, and A to area. This gave a volume of 0.494 hm^3 which was used for THV. If the depths had spanned more than one 2.5 m interval, volumes for individual intervals would have been summed. Total lake volume was calculated by summing the volumes of all the "slices" (4.094 hm^3).

Appendix Table B. Mean fork length-at-age (upper values) and sample sizes (lower values) for each of 47 lakes in Ontario and estimates of L_∞' and K' by an empirical method (see text).

Lake Name	Distance code	Lat	Long	Area (ha)	Ageing method	Sample size Total	Sample size L_∞'	L_∞'	K'	Fork length (cm) and sample size at annulus 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Plank	41	4655	8247	951	Scale	2142	3	64.0	0.166			27.7	51.9	54.9	60.4	66.4	55.1	66.5	71.6															
												24	366	744	936	89	1	1	1															
Louise	51	4528	7829	531	Scale	571	14	49.5	0.237				28.7	34.1	37.3	40.5	41.3	47.5	56.1	53.9													
													9	107	254	146	41	10	2	2													
Dickey	66	4647	7746	214	Scale	240	15	40.4	0.305		22.2	17.8	25.3	29.8	33.6	38.5	40.2	41.1															
											1	1	12	40	93	78	11	4															
Kenisis	54	4513	7838	1360	Scale	312	6	56.2	0.143				24.5	28.9	34.5	39.7	44.0	49.7	50.6	54.5	60.9												
													14	66	80	79	49	18	2	1	3												
Big Salmon	64	4432	7830	148	Scale	225	10	59.4	0.168			27.5	29.0	33.2	38.7	41.1	47.9	54.7	59.4															
												4	29	45	48	45	27	17	10															
Spruce	25	4831	9033	384	Ontario	1000	5	55.0	0.137	9.5	14.5	17.9	23.5	27.4	31.0	33.7	37.0	38.3	40.1	40.6	42.6	42.9	44.0	49.3	42.6	42.8	46.4	44.4	46.1	46.3	55.4	48.9	54.5		43.5
										1	6	24	54	105	149	105	142	115	83	61	40	32	15	15	16	15	5	9	5	5	3	3	2		1
Big Clear	64	4633	7638	187	Scale	264	13	47.9	0.241			25.2	28.8	31.0	36.8	41.9	41.9	45.5	57.1															
												10	58	87	48	27	21	10	3															
Devil	64	4635	7627	1061	Scale	272	14	58.8	0.198			25.6	30.7	34.8	42.8	46.5	50.9	58.8																
												15	61	64	59	38	21	14																
Snake	51	4531	7841	607	Scale	282	9	76.3	0.110			19.9	25.2	30.6	36.3	42.9	51.4	58.2	61.3	63.2	70.4	75.0	76.8	74.8	80.0	81.7								
												2	17	58	45	48	30	21	20	15	7	7	3	7	1	1								
Gimmerwee	25	4834	9026	3080	Ontario	175	9	58.4	0.162	13.6	20.2	24.3	28.8	33.0	36.7	38.1	43.6	46.4	45.0	50.0	51.1	57.0		53.2			65.8				49.0	58.9		68.7
										1	3	7	8	27	32	16	20	20	15	10	8	4		2			1				1	1		1
Charleston	61	4632	7600	2517	Scale	285	6	64.9	0.181			16.0	27.4	32.5	38.3	42.3	48.4	59.2	66.8	61.2														
												1	13	59	75	83	36	16	4	2														
Little Gull	21	4905	9136	325	Ontario	51	3	50.3	0.157			15.0	17.8	23.7	33.2	33.3	35.6	43.4	41.4	49.8	48.9	45.4	36.9	46.9	57.4			52.2		60.3		56.1			
												22	3	1	3	4	7	11	6	2	2	2	1	2	1			1		2		1			
Big Salmon	61	4445	7413	5701	Scale	270	4	62.1	0.233				25.9	35.0	41.2	46.8	52.5	56.8	55.1	62.1															
													6	57	79	56	32	22	14	4														
Eagle	11	4942	9313	27681	Scale	35	3	78.4	0.115						35.5		43.7	48.9	51.4	60.0	66.4	71.7	79.3	78.4											
															3		6	2	3	2	6	5	5	3										
Joseph	35	4511	7947	4972	Scale	602	6	72.0	0.112				30.0	34.3	39.3	34.7	48.4	47.7	51.8	56.3	62.0	64.9	66.2	70.9	74.3										
													1	11	85	45	97	90	140	64	25	17	10	4	2									
Muskoka	35	4500	7925	10521	Scale	133	7	66.0	0.168					32.9	37.3	36.0	48.3	53.4	57.4	60.6	66.0	58.2												
														5	9	3	28	20	25	22	7	14												
Lake of the Woods	14	4830	9420	29500	Ontario	100	7	81.5	0.137			21.9	29.0	36.5	43.9	53.7	57.2	63.6	68.1	70.1	73.4	79.2	79.3	80.2	81.0			89.6		84.6					
												3	4	23	31	27	25	25	10	14	12	5	3	3	2			1		1					
Rawson	35	4510	7935	5827	Scale	111	9	64.9	0.200					42.9	48.8	47.6	53.4	55.5	59.0	60.6	64.1	56.1	71.9											
														3	11	20	15	19	6	9	8	19	1											

Appendix Table B (cont'd). Mean fork length-at-age (upper values) and sample sizes (lower values) for each of 47 lakes in Ontario and estimates of L_∞' and K'.

Lake name	District code	Lat	Long	Surface area (ha)	Ageing method	Sample Size Total	Sample Size L_∞'	L_∞'	K'	Fork length (mm) and sample size at summed age 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Tamagami	46	4700	8000	20971	Scale	344	7	79.3	0.137			27.2	31.9	35.1	43.2	52.7	59.0	63.9	72.6	85.0	88.5	94.0											
												18	9	63	129	69	42	7	4	1	1	1											
Pickerel	25	4837	9119	6058	Otolith	174	8	67.0	0.121		14.9	22.9	30.0	28.2	35.3	37.5	43.1	46.4	47.9	48.1	54.6	57.8	55.3	60.0	59.3	59.7	62.5	60.4	75.5	62.8	67.1			67.2	
											1	3	5	12	20	20	25	19	15	12	8	7	6	3	4	4	1	4	1	1	3			2	
Robinson	21	4811	9139	421	Otolith	45	2	61.6	0.164			23.0	23.8	33.0	40.3		48.1	42.0	47.2	46.7	53.7	48.2	55.9		56.0	55.3		58.9	56.6			54.8		57.4	61.4
												2	1	1	2		1	7	5	3	4	1	1		2	1		1	1			2		5	1
Gang	44	4705	8332	383	Scale	79	4	81.2	0.127		19.4	26.3	31.6	36.9	42.0	51.4	57.2	63.5	69.6	80.5	88.0												
											2	4	15	26	15	9	3	1	1	1	2												
Onaman	44	4710	8340	260	Scale	111	7	54.0	0.182		19.8	22.8	28.1	30.8	38.7		54.5		72.0	82.0													
											1	28	41	14	3		1		2	1													
Lowville	31	4931	7814	2402	Scale	569	9	79.2	0.116			38.9	52.3	52.2	58.8	64.5	69.1	72.5	74.3	78.1		69.9	79.1	75.1	82.1	86.5							
												1	1	18	63	151	170	127	21	4		4	4	2	2	1							
Opeongo	31	4842	7820	5860	Scale	6015	7	87.2	0.092		16.9	20.9	26.9	31.0	36.8	42.2	48.5	53.9	59.3	62.9	65.4	67.2	71.8	72.1	79.7	86.7	88.6						
											5	181	411	873	1114	985	965	613	312	225	198	125	49	25	11	5	2					
Little Joe	11	5022	9337	221	Otolith	86	6	59.9	0.207	23.8	26.8	30.4	34.5	38.6	41.6	46.1	52.3	55.1	59.9	57.9	52.7	52.4	59.7										
										5	9	9	11	12	7	6	7	5	6	5	1	2	1										
South Otterskin	12	4913	9338	214	Otolith	85	3	60.7	0.210			26.0	34.0	37.0	43.4	47.1	50.8	54.5	55.7	56.8	60.2	59.9		61.0									
												3	4	4	15	19	18	8	7	2	1	2		2									
Islets	13	4913	9216	189	Otolith	92	6	52.7	0.229	19.8	23.7	28.9	31.9	36.1	39.7	41.8	44.8	46.7	48.5	47.4	50.6	51.5	52.1	52.7									
										1	2	7	5	6	5	6	7	5	6	9	12	8	7	6									
Burnt Island	25	4847	9051	119	Otolith	75	5	54.2	0.160			25.5	27.8	31.4	33.1	34.9	38.7	42.1	45.1	46.7	48.6	51.6	52.7	56.5									
												6	11	9	7	9	7	6	6	2	3	4	3	2									
Greenwich	25	4848	8851	484	Otolith	264	13	43.7	0.242	3.9	20.4	23.9	25.9	30.0	32.3	37.0	35.4	39.4	37.8	40.1	42.1	43.7	42.5	41.9									
										7	14	14	25	15	23	20	20	23	21	22	17	13	14	6									
Loch Erne	25	4837	9021	165	Otolith	108	6	60.2	0.154	14.8	18.1	25.0	31.6	34.2	35.7	38.5	45.2	50.5	56.3	58.3	58.1	60.2	59.7										
										5	6	16	8	6	9	13	14	9	6	4	3	6	3										
Children	41	4621	8305	2589	Scale	1255	5	70.6	0.167			28.7	32.2	37.9	43.7	51.7	59.6	66.1	70.6														
												2	77	287	592	220	56	16	5														
Christmas	41	4635	8244	58	Scale	204	17	50.9	0.305			23.4	30.5	25.6	43.2	49.7	56.6	65.8															
												1	29	103	54	15	1	1															
Sandwhite	41	4635	8241	305	Scale	605	8	61.1	0.168			24.1	29.8	33.7	39.5	45.6	56.2	62.7	71.6		77.5												
												9	89	296	102	21	5	1	1		1												
Wakwekobi	41	4619	8324	2708	Scale	258	4	74.8	0.174				33.1	40.8	46.7	53.7	59.5	64.3	72.4	82.5														
													3	14	41	76	112	28	3	1													
Adelaide	44	4704	8418	137	Scale	299	7	45.8	0.291			20.8	28.5	33.4	43.3	53.9																	
												13	99	180	6	1																	

Appendix Table B (cont'd). Mean fork length-at-age (upper values) and sample sizes (lower values) for each of 47 lakes in Ontario and estimates of L_∞' and K'.

Lake name	District code	Lat	Long	Surface area (ha)	Ageing method	Sample Size Total	L_∞'	K'	Fork length (cm) and sample size at summed age 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Bone	44	4648	8416	123	Scale	708	7	43.0	0.250			20.5	25.1	31.2	36.7	40.3	50.7																	
												71	371	218	41	5	2																	
Bunger	44	4654	8354	2255	Scale	201	6	55.5	0.205		22.0	24.6	30.4	36.9	45.1	47.7	51.0		64.3															
											4	31	67	76	46	21	5		1															
Nelson	45	4644	8305	316	Scale	410	10	61.9	0.151			21.5	25.6	34.9	35.8	42.9	50.9	62.5	60.6															
												14	156	139	81	14	2	7	3															
Happy Isle	51	4545	7830	536	Scale	2990	11	58.2	0.157				26.9	32.5	36.3	38.3	41.9	47.0	50.8	58.2															
													14	107	955	1177	541	193	35	11														
Wollaston	52	4451	7750	580	Scale	153	12	60.2	0.258			15.6	21.4	27.1	30.9	34.7	40.0	43.0																
												4	11	29	49	48	11	1																
Kawagama	53	4518	7845	2819	Scale	153	6	48.8	0.346				26.1	30.7	33.7	41.8	44.9	46.8	60.1															
													5	36	50	53	17	5	1															
Lake of Bays	55	4515	7904	7053	Scale	51	3	68.8	0.120					32.9	51.6	45.8	44.8	54.8	57.1	59.8	69.8	66.1	68.3											
														1	7	3	8	15	12	3	1	1	2											
Muskoka	54	4505	7819	260	Scale	94	4	55.8	0.193				22.9	30.1	38.7	41.7	46.3	47.2		60.9			71.7											
													5	5	33	28	19	2		1			1											
Bracebridge	54	4504	7844	716	Scale	132	7	63.2	0.134			23.0	22.8	28.9	34.5	40.3	45.9	51.1	56.7	60.9	60.9	69.4												
												4	37	35	20	13	9	7	2	5	2	2											
Gull	54	4431	7847	995	Scale	447	9	54.5	0.164			23.8	26.6	29.5	33.9	39.2	43.3	53.6		60.0	63.7													
												2	46	167	161	33	9	7		1	1													
Redstone	54	4511	7832	1193	Scale	80	5	48.8	0.205					28.5	33.0	38.3	42.2	47.7	53.5															
													17	19	26	13	4	1															

Appendix C. Example of the "empirical" method of calculating von Bertalanffy parameters.

The method described here was used to estimate L_∞' and K' for the set of 47 Ontario lakes found in Appendix Table B. Note that it is preferable to use this method with length and age data pertaining to individual fish. We had to make do with mean length-at-age, which was an average (weighted by sample size) of the five most recent years of information (if available). Louisa Lake will be used as an example. The following are averaged data from 1978-1982:

Age	Fork length (cm)	n
4	28.7	9
5	34.1	107
6	37.3	254
7	40.5	146
8	44.3	41
9	47.5	10
10	56.1	2
11	53.9	2

Ideally, we want the geometric mean of the longest lengths making up 5% of of the sample or 10 fish, whichever is less, for the estimate of L_∞'. In this case, we want 10 fish. Ages 10 and 11 have 4 fish (note that age 10 has the longest mean length), meaning 6 more are required to meet the required sample size. It was decided to include the longest age-classes up to the sample size that was closest to the one desired. So, in this case, we included age 9, giving a final sample size of 14. Fourteen is closer to 10 than 4. The small sample size was used for ties. The weighted geometric mean then gives

$$L_\infty' = \text{antilog}\left[\frac{(2(\log 56.1) + 2(\log 53.9) + 10(\log 47.5))}{14}\right] = 49.5$$

The slope for a weighted regression of $y = -\ln(1 - Lt/L)$ on $x = t$ ($t = 4,\ldots,7$), forced through the origin, gives the estimate for K':

x	y	n	nx^2	nxy
4	0.867	9	144	31.2
5	1.168	107	2675	624.9
6	1.401	254	9144	2135.1
7	1.705	146	7154	1742.5
Σ			19117	4533.7

$$K' = \frac{4533.7}{19117} = 0.237$$

Appendix Table D. Lake trout mean fork length- and weight-at-age and derived "a" and "b" parameters for the weight-length function for 23 lakes in Ontario.

Lake name	Lat	Long	Statistic	Age in years																				Weight-length relation			
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	n	a (10^{-6})	b	r^2
Little Joe	5002	9537	Length(mm)	270	366	384	505	586	616	681	523	551	599													86	1.89	3.31	.989
			Weight (g)	152	399	501	673	861	885	1306	1687	175	2812													86			
L. o' Woods	4950	9420	Length(mm)			219	290	363	439	537	572	636	691	701	754	782										199	3.26	3.21	.989
			Weight (g)			100	203	533	953	1825	2502	125	4067	4497	5150	6057										206			
S Otonabee	4913	9358	Length(mm)			260	340	370	434	471	508	545	557													85	1.35	3.36	1.000
			Weight (g)			176	427	572	983	1294	1639	043	2540													85			
Iskwa	4913	9216	Length(mm)	198	237	289	319	361	397	418	440	467	483	474	506	515	521	527								91	5.88	3.17	.987
			Weight (g)	70	136	270	332	492	641	827	937	133	1195	1102	1446	1571	1613	1607								92			
Gamewish	4848	9851	Length(mm)		264	259	259	300	323	370	354	394	378	401	421	437	420	419								257	4.07	3.17	.988
			Weight (g)		86	137	179	294	378	562	697	697	613	674	850	888	910	854								257			
Burnt Island	4847	9851	Length(mm)			255	270	314	331	349	387	421	451	467	486	514	527	540								75	2.78	3.23	.998
			Weight (g)			171	223	330	385	469	644	796	995	1218	1280	1438	1457	2258								75			
Pickerel	4837	9119	Length(mm)		149	229	300	292	353	375	431	464	479	481	546	578	533		593	597	625	684	733	628	651	172	5.57	3.12	.995
			Weight (g)		39	133	348	335	559	618	992	260	1312	1364	2220	1960	2620		2476	2849	2230	2943	5209	3050	3500	170			
Loch Erne	4837	9021	Length(mm)	148	161	259	316	342	357	385	452	505	562	583	581	602	587									108	1.18	3.37	.998
			Weight (g)	32	57	151	305	401	495	602	1 057	517	2257	2578	2662	2613	2839									108			
Gamewarra	4836	9038	Length(mm)	134	203	243	288	330	367	381	436	464	488	500	511	570										172	7.47	3.09	.989
			Weight (g)	38	82	139	362	448	636	728	1000	269	1218	1575	1853	2730										170			
Onaisis	4710	8940	Length(mm)		198	220	281	308	387		545		720	820												111	3.54	3.20	.995
			Weight (g)		70	119	254	440	707		2140		3550	6940												111			
Gang	4705	8552	Length(mm)		194	263	316	369	420	514	572	635	696	805	880											79	10.04	3.03	.996
			Weight (g)		85	221	389	561	910	1632	1985	880	3590	7730	7880											79			
Adelaide	4706	8418	Length(mm)			208	285	334	423	559																399	.85	3.42	.998
			Weight (g)			68	197	448	816	1725																326			
Ranger	4654	8554	Length(mm)		220	246	304	367	426	470	559															189	4.42	3.10	.996
			Weight (g)		80	113	221	419	655	950	1310															189			
Wahwahshe	4647	8850	Length(mm)				331	408	467	537	595	643	724													278	.59	3.50	.999
			Weight (g)				372	776	1308	2150	2999	814	3676													265			
Bass	4648	8436	Length(mm)			299	356	311	367																	357	4.03	3.18	1.000
			Weight (g)			95	183	334	582																	351			
Flesh	4655	8547	Length(mm)			267	333	382	448	482																77	2.35	3.28	.996
			Weight (g)			250	383	660	1250	1445																**			
Chimmo	4655	8344	Length(mm)			254	305	356	402	497	566	658														204	4.79	3.15	.998
			Weight (g)			140	324	534	971	1505	2540	480														196			
Smoorie	4655	8341	Length(mm)			241	298	337	395	456	562		716													405	.82	3.44	.998
			Weight (g)			123	380	424	673	1180	2141		3720													389			
Oshkow	4651	8303	Length(mm)			287	322	379	457	517	596	661	786													1255	6.80	3.10	.994
			Weight (g)			270	359	560	837	1497	2366	208	4534													1060			

Appendix Table D (Cont'd). Lake trout mean fork length- and weight-at-age and derived "a" and "b" parameters for the weight-length function for 23 lakes in Ontario.

Lake name	Lat	Long	Statistic	Age in years																				Weight-length relation			
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	n	a(10^{-6})	b	r^2
Opasatika	4542	7823	Length(mm)		169	259	280	310	360	422	485	539	595	629	654	672	718	721	797	847						6013	2.60	3.23	.997
			Weight (g)		47	114	166	330	556	854	1360	964	2702	3501	3830	4221	5308	5127	6681	9859						4687			
Lake Joseph	4511	7949	Length(mm)			280	243	293	339	384	442	518	577	589	662	664	695	743								401	6.71	3.08	.995
			Weight (g)			160	120	230	380	672	939	519	1905	2371	3406	3355	3475	4500								401			
Wallstone	4451	7759	Length(mm)			156	214	271	309	367	400	450														153	375.61	2.40	.997
			Weight (g)			70	150	230	360	470	660	880														153			
Dickey	4447	7744	Length(mm)				255	298	336	385	402	411														256	348.52	2.47	.988
			Weight (g)				189	313	418	612	681	798														256			
All lakes			Length(mm)	180	302	260	292	358	390	443	492	526	583	586	598	593	576	595	695	752	620	604	755	620	671		4.12	3.18	.995
			Weight (g)	66	88	154	278	445	713	1086	1506	1914	2899	2993	3530	3643	3578	3199	4584	6254	2750	2963	5200	3050	3333				
			Data sets	4	10	21	20	23	23	21	20	17	16	11	10	9	7	5	2	2	1	1	1	1	1				

Appendix Table B-1. Calculated[1] natural mortality (M) values for combinations of K and L_∞ and T = 6°C.

	Values of K																	
L_∞	0.06	0.08	0.10	0.12	0.14	0.16	0.18	0.20	0.22	0.24	0.26	0.28	0.30	0.32	0.34	0.36	0.38	0.40
40	0.12	0.15	0.17	0.20	0.22	0.24	0.26	0.27	0.29	0.31	0.33	0.34	0.36	0.37	0.39	0.40	0.42	0.43
42	0.12	0.15	0.17	0.19	0.21	0.23	0.25	0.27	0.29	0.31	0.32	0.34	0.35	0.37	0.38	0.40	0.41	0.43
44	0.12	0.15	0.17	0.19	0.21	0.23	0.25	0.27	0.28	0.30	0.32	0.33	0.35	0.36	0.38	0.39	0.41	0.42
46	0.12	0.14	0.17	0.19	0.21	0.23	0.25	0.26	0.28	0.30	0.31	0.33	0.34	0.36	0.37	0.39	0.40	0.42
48	0.12	0.14	0.17	0.19	0.21	0.23	0.24	0.26	0.28	0.29	0.31	0.33	0.34	0.35	0.37	0.38	0.40	0.41
50	0.12	0.14	0.16	0.18	0.20	0.22	0.24	0.26	0.27	0.29	0.31	0.32	0.34	0.35	0.36	0.38	0.39	0.41
52	0.12	0.14	0.16	0.18	0.20	0.22	0.24	0.26	0.27	0.29	0.30	0.32	0.33	0.35	0.36	0.37	0.39	0.40
54	0.11	0.14	0.16	0.18	0.20	0.22	0.24	0.25	0.27	0.28	0.30	0.31	0.33	0.34	0.36	0.37	0.38	0.40
56	0.11	0.14	0.16	0.18	0.20	0.22	0.23	0.25	0.27	0.28	0.30	0.31	0.33	0.34	0.35	0.37	0.38	0.39
58	0.11	0.14	0.16	0.18	0.20	0.21	0.23	0.25	0.26	0.28	0.29	0.31	0.32	0.34	0.35	0.36	0.38	0.39
60	0.11	0.13	0.16	0.18	0.19	0.21	0.23	0.25	0.26	0.28	0.29	0.31	0.32	0.33	0.35	0.36	0.37	0.39
62	0.11	0.13	0.15	0.17	0.19	0.21	0.23	0.24	0.26	0.27	0.29	0.30	0.32	0.33	0.34	0.36	0.37	0.38
64	0.11	0.13	0.15	0.17	0.19	0.21	0.22	0.24	0.26	0.27	0.29	0.30	0.31	0.33	0.34	0.35	0.37	0.38
66	0.11	0.13	0.15	0.17	0.19	0.21	0.22	0.24	0.25	0.27	0.28	0.30	0.31	0.32	0.34	0.35	0.36	0.38
68	0.11	0.13	0.15	0.17	0.19	0.20	0.22	0.24	0.25	0.27	0.28	0.29	0.31	0.32	0.33	0.35	0.36	0.37
70	0.11	0.13	0.15	0.17	0.19	0.20	0.22	0.23	0.25	0.26	0.28	0.29	0.31	0.32	0.33	0.34	0.36	0.37
72	0.11	0.13	0.15	0.17	0.18	0.20	0.22	0.23	0.25	0.26	0.28	0.29	0.30	0.32	0.33	0.34	0.35	0.37
74	0.11	0.13	0.15	0.17	0.18	0.20	0.22	0.23	0.25	0.26	0.27	0.29	0.30	0.31	0.33	0.34	0.35	0.36
76	0.10	0.13	0.15	0.16	0.18	0.20	0.21	0.23	0.24	0.26	0.27	0.29	0.30	0.31	0.32	0.34	0.35	0.36
78	0.10	0.13	0.14	0.16	0.18	0.20	0.21	0.23	0.24	0.26	0.27	0.28	0.30	0.31	0.32	0.33	0.35	0.36
80	0.10	0.12	0.14	0.16	0.18	0.20	0.21	0.23	0.24	0.25	0.27	0.28	0.29	0.31	0.32	0.33	0.34	0.36
82	0.10	0.12	0.14	0.16	0.18	0.19	0.21	0.22	0.24	0.25	0.27	0.28	0.29	0.31	0.32	0.33	0.34	0.35
84	0.10	0.12	0.14	0.16	0.18	0.19	0.21	0.22	0.24	0.25	0.26	0.28	0.29	0.30	0.32	0.33	0.34	0.35
86	0.10	0.12	0.14	0.16	0.18	0.19	0.21	0.22	0.24	0.25	0.26	0.28	0.29	0.30	0.31	0.33	0.34	0.35
88	0.10	0.12	0.14	0.16	0.17	0.19	0.21	0.22	0.23	0.25	0.26	0.27	0.29	0.30	0.31	0.32	0.34	0.35
90	0.10	0.12	0.14	0.16	0.17	0.19	0.20	0.22	0.23	0.25	0.26	0.27	0.29	0.30	0.31	0.32	0.33	0.34
92	0.10	0.12	0.14	0.16	0.17	0.19	0.20	0.22	0.23	0.25	0.26	0.27	0.28	0.30	0.31	0.32	0.33	0.34
94	0.10	0.12	0.14	0.15	0.17	0.19	0.20	0.22	0.23	0.24	0.26	0.27	0.28	0.29	0.31	0.32	0.33	0.34
96	0.10	0.12	0.14	0.15	0.17	0.19	0.20	0.21	0.23	0.24	0.26	0.27	0.28	0.29	0.30	0.32	0.33	0.34

[1] $\log M = -0.279 \log(1.094 \log(L_\infty)) + 0.6543 \log K + 0.3537$ where L_∞ is in fork length (cm).

Appendix Table B-2. Calculated[1] values for the ratio M/K for combinations of K and L_∞ and T = 6°C.

L_∞	Values of K																	
	0.06	0.07	0.08	0.09	0.10	0.11	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.21	0.22	0.23
40	2.08	1.97	1.88	1.81	1.74	1.69	1.64	1.59	1.55	1.52	1.48	1.45	1.42	1.40	1.37	1.35	1.33	1.31
42	2.05	1.95	1.86	1.78	1.72	1.66	1.62	1.57	1.53	1.50	1.46	1.43	1.40	1.38	1.35	1.33	1.31	1.29
44	2.03	1.92	1.83	1.76	1.70	1.64	1.59	1.55	1.51	1.48	1.44	1.41	1.39	1.36	1.34	1.31	1.29	1.27
46	2.00	1.90	1.81	1.74	1.68	1.62	1.57	1.53	1.49	1.46	1.43	1.40	1.37	1.34	1.32	1.30	1.28	1.26
48	1.98	1.87	1.79	1.72	1.66	1.60	1.56	1.51	1.48	1.44	1.41	1.38	1.35	1.33	1.30	1.28	1.26	1.24
50	1.96	1.85	1.77	1.70	1.64	1.59	1.54	1.50	1.46	1.42	1.39	1.36	1.34	1.31	1.29	1.27	1.25	1.23
52	1.95	1.83	1.75	1.68	1.62	1.57	1.52	1.48	1.44	1.41	1.38	1.35	1.32	1.30	1.28	1.25	1.23	1.22
54	1.91	1.81	1.73	1.66	1.60	1.55	1.51	1.46	1.43	1.39	1.36	1.34	1.31	1.28	1.26	1.24	1.22	1.20
56	1.89	1.80	1.72	1.65	1.59	1.54	1.49	1.45	1.41	1.38	1.35	1.32	1.30	1.27	1.25	1.23	1.21	1.19
58	1.88	1.78	1.70	1.63	1.57	1.52	1.48	1.44	1.40	1.37	1.34	1.31	1.28	1.26	1.24	1.22	1.20	1.18
60	1.86	1.76	1.68	1.62	1.56	1.51	1.46	1.42	1.39	1.35	1.32	1.30	1.27	1.25	1.23	1.21	1.19	1.17
62	1.84	1.75	1.67	1.60	1.54	1.49	1.45	[illegible]	1.37	1.34	1.31	1.28	1.26	1.24	1.21	1.19	1.18	1.16
64	1.83	1.73	1.65	1.59	1.53	1.48	1.44	1.40	1.36	1.33	1.30	1.27	1.25	1.23	1.20	1.18	1.16	1.15
66	1.81	1.72	1.64	1.57	1.52	1.47	1.42	1.39	1.35	1.32	1.29	1.26	1.24	1.21	1.19	1.17	1.15	1.14
68	1.79	1.70	1.62	1.56	1.50	1.46	1.41	1.37	1.34	1.31	1.28	1.25	1.23	1.20	1.18	1.16	1.15	1.13
70	1.78	1.69	1.61	1.55	1.49	1.44	1.40	1.36	1.33	1.30	1.27	1.24	1.22	1.19	1.17	1.15	1.14	1.12
72	1.77	1.67	1.60	1.54	1.48	1.43	1.39	1.35	1.32	1.29	1.26	1.23	1.21	1.19	1.16	1.15	1.13	1.11
74	1.75	1.66	1.59	1.52	1.47	1.42	1.38	1.34	1.31	1.28	1.25	1.22	1.20	1.18	1.16	1.14	1.12	1.10
76	1.74	1.65	1.57	1.51	1.46	1.41	1.37	1.33	1.30	1.27	1.24	1.21	1.19	1.17	1.15	1.13	1.11	1.09
78	1.73	1.64	1.56	1.50	1.45	1.40	1.36	1.32	1.29	1.26	1.23	1.20	1.18	1.16	1.14	1.12	1.10	1.09
80	1.71	1.63	1.55	1.49	1.44	1.39	1.35	1.31	1.28	1.25	1.22	1.20	1.17	1.15	1.13	1.11	1.09	1.08
82	1.70	1.61	1.54	1.48	1.43	1.38	1.34	1.30	1.27	1.24	1.21	1.19	1.16	1.14	1.12	1.10	1.09	1.07
84	1.69	1.60	1.53	1.47	1.42	1.37	1.33	1.29	1.26	1.23	1.21	1.18	1.16	1.14	1.12	1.10	1.08	1.06
86	1.68	1.59	1.52	1.46	1.41	1.36	1.32	1.29	1.25	1.22	1.20	1.17	1.15	1.13	1.11	1.09	1.07	1.06
88	1.67	1.58	1.51	1.45	1.40	1.35	1.31	1.28	1.25	1.22	1.19	1.17	1.14	1.12	1.10	1.08	1.07	1.05
90	1.66	1.57	1.50	1.44	1.39	1.35	1.31	1.27	1.24	1.21	1.18	1.16	1.14	1.11	1.09	1.08	1.06	1.04
92	1.65	1.56	1.49	1.43	1.38	1.34	1.30	1.26	1.23	1.20	1.18	1.15	1.13	1.11	1.09	1.07	1.05	1.04
94	1.64	1.55	1.48	1.43	1.37	1.33	1.29	1.25	1.22	1.19	1.17	1.14	1.12	1.10	1.08	1.06	1.05	1.03
96	1.63	1.55	1.48	1.42	1.37	1.32	1.28	1.25	1.22	1.19	1.16	1.14	1.11	1.09	1.07	1.06	1.04	1.02

[1] $\log \frac{M}{K} = 0.3537 - 0.3457 \log K - 0.279 \log(1.894 \log L_\infty)$

Appendix Table B-2 (cont'd). Calculated values for the ratio M/K for combinations of K and L_m and T = 6°C.

	Values of K																
L_m	0.24	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.34	0.35	0.36	0.37	0.38	0.39	0.40
40	1.29	1.27	1.25	1.24	1.22	1.21	1.19	1.18	1.17	1.15	1.14	1.13	1.12	1.11	1.10	1.09	1.08
42	1.27	1.25	1.24	1.22	1.21	1.19	1.18	1.16	1.15	1.14	1.13	1.12	1.10	1.09	1.08	1.07	1.07
44	1.25	1.24	1.22	1.20	1.19	1.18	1.16	1.15	1.14	1.12	1.11	1.10	1.09	1.08	1.07	1.06	1.05
46	1.24	1.22	1.21	1.19	1.17	1.16	1.15	1.13	1.12	1.11	1.10	1.09	1.08	1.07	1.06	1.05	1.04
48	1.22	1.21	1.19	1.18	1.16	1.15	1.13	1.12	1.11	1.10	1.09	1.07	1.06	1.05	1.04	1.04	1.03
50	1.21	1.19	1.18	1.16	1.15	1.13	1.12	1.11	1.10	1.08	1.07	1.06	1.05	1.04	1.03	1.02	1.01
52	1.20	1.18	1.16	1.15	1.14	1.12	1.11	1.10	1.08	1.07	1.06	1.05	1.04	1.03	1.02	1.01	1.00
54	1.19	1.17	1.15	1.14	1.12	1.11	1.10	1.08	1.07	1.06	1.05	1.04	1.03	1.02	1.01	1.00	0.99
56	1.17	1.16	1.14	1.13	1.11	1.10	1.09	1.07	1.06	1.05	1.04	1.03	1.02	1.01	1.00	0.99	0.98
58	1.16	1.15	1.13	1.12	1.10	1.09	1.08	1.06	1.05	1.04	1.03	1.02	1.01	1.00	0.99	0.98	0.97
60	1.15	1.13	1.12	1.10	1.09	1.08	1.07	1.05	1.04	1.03	1.02	1.01	1.00	0.99	0.98	0.97	0.96
62	1.14	1.12	1.11	1.09	1.08	1.07	1.06	1.04	1.03	1.02	1.01	1.00	0.99	0.98	0.97	0.96	0.96
64	1.13	1.11	1.10	1.09	1.07	1.06	1.05	1.03	1.02	1.01	1.00	0.99	0.98	0.97	0.96	0.96	0.95
66	1.12	1.10	1.09	1.08	1.06	1.05	1.04	1.03	1.01	1.00	0.99	0.98	0.97	0.96	0.96	0.95	0.94
68	1.11	1.10	1.08	1.07	1.05	1.04	1.03	1.02	1.01	1.00	0.99	0.98	0.97	0.96	0.95	0.94	0.93
70	1.10	1.09	1.07	1.06	1.05	1.03	1.02	1.01	1.00	0.99	0.98	0.97	0.96	0.95	0.94	0.93	0.92
72	1.09	1.08	1.06	1.05	1.04	1.02	1.01	1.00	0.99	0.98	0.97	0.96	0.95	0.94	0.93	0.92	0.92
74	1.09	1.07	1.06	1.04	1.03	1.02	1.00	0.99	0.98	0.97	0.96	0.95	0.94	0.93	0.93	0.92	0.91
76	1.08	1.06	1.05	1.03	1.02	1.01	1.00	0.99	0.98	0.96	0.96	0.95	0.94	0.93	0.92	0.91	0.90
78	1.07	1.05	1.04	1.03	1.01	1.00	0.99	0.98	0.97	0.96	0.95	0.94	0.93	0.92	0.91	0.90	0.90
80	1.06	1.05	1.03	1.02	1.01	0.99	0.98	0.97	0.96	0.95	0.94	0.93	0.92	0.91	0.91	0.90	0.89
82	1.05	1.04	1.03	1.01	1.00	0.99	0.98	0.97	0.95	0.94	0.94	0.93	0.92	0.91	0.90	0.89	0.88
84	1.05	1.03	1.02	1.01	0.99	0.98	0.97	0.96	0.95	0.94	0.93	0.92	0.91	0.90	0.89	0.89	0.88
86	1.04	1.03	1.01	1.00	0.99	0.97	0.96	0.95	0.94	0.93	0.92	0.91	0.90	0.90	0.89	0.88	0.87
88	1.03	1.02	1.01	0.99	0.98	0.97	0.96	0.95	0.94	0.93	0.92	0.91	0.90	0.89	0.88	0.87	0.87
90	1.03	1.01	1.00	0.99	0.97	0.96	0.95	0.94	0.93	0.92	0.91	0.90	0.89	0.88	0.88	0.87	0.86
92	1.02	1.01	0.99	0.98	0.97	0.96	0.95	0.93	0.92	0.91	0.91	0.90	0.89	0.88	0.87	0.86	0.86
94	1.02	1.00	0.99	0.97	0.96	0.95	0.94	0.93	0.92	0.91	0.90	0.89	0.88	0.87	0.87	0.86	0.85
96	1.01	1.00	0.98	0.97	0.96	0.95	0.93	0.92	0.91	0.90	0.89	0.89	0.88	0.87	0.86	0.85	0.85

Appendix Table B.3. Calculated optimal relative recruitment length (L_c) and fishing mortality (F) for M/K ratios in the range 0.2-3.0 and natural mortality rates (M) in the range 0.10-0.35. (L_c is expressed as a decimal fraction of L_∞.

		Natural mortality (M) values												
M/K	L_c	0.10	0.11	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.21	0.22
0.2	0.86	0.18	0.19	0.21	0.23	0.25	0.26	0.28	0.30	0.32	0.34	0.35	0.37	0.39
0.3	0.83	0.17	0.18	0.20	0.22	0.23	0.25	0.27	0.28	0.30	0.32	0.33	0.35	0.37
0.4	0.80	0.16	0.17	0.19	0.21	0.22	0.24	0.25	0.27	0.28	0.30	0.32	0.33	0.35
0.5	0.78	0.15	0.16	0.18	0.19	0.21	0.22	0.24	0.25	0.27	0.28	0.30	0.31	0.33
0.6	0.75	0.14	0.16	0.17	0.19	0.20	0.21	0.23	0.24	0.26	0.27	0.29	0.30	0.31
0.7	0.73	0.14	0.15	0.16	0.18	0.19	0.21	0.22	0.23	0.25	0.26	0.27	0.29	0.30
0.8	0.71	0.13	0.15	0.16	0.17	0.18	0.20	0.21	0.22	0.24	0.25	0.26	0.28	0.29
0.9	0.69	0.13	0.14	0.15	0.17	0.18	0.19	0.20	0.22	0.23	0.24	0.25	0.27	0.28
1.0	0.67	0.12	0.14	0.15	0.16	0.17	0.18	0.20	0.21	0.22	0.23	0.25	0.26	0.27
1.1	0.65	0.12	0.13	0.14	0.16	0.17	0.18	0.19	0.20	0.22	0.23	0.24	0.25	0.26
1.2	0.63	0.12	0.13	0.14	0.15	0.16	0.17	0.19	0.20	0.21	0.22	0.23	0.24	0.26
1.3	0.61	0.11	0.12	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.22	0.23	0.24	0.25
1.4	0.60	0.11	0.12	0.13	0.14	0.16	0.17	0.18	0.19	0.20	0.21	0.22	0.23	0.24
1.5	0.58	0.11	0.12	0.13	0.14	0.15	0.16	0.17	0.19	0.20	0.21	0.22	0.23	0.24
1.6	0.57	0.11	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.21	0.22	0.24
1.7	0.56	0.11	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.21	0.22	0.23
1.8	0.54	0.10	0.11	0.12	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.21	0.22	0.23
1.9	0.53	0.10	0.11	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.21	0.22	0.23
2.0	0.52	0.10	0.11	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.21	0.22
2.1	0.51	0.10	0.11	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.21	0.22
2.2	0.50	0.10	0.11	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.21	0.22
2.3	0.49	0.10	0.11	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.21	0.22
2.4	0.48	0.10	0.11	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.21	0.22
2.5	0.47	0.10	0.11	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.21	0.22
2.6	0.46	0.10	0.11	0.12	0.13	0.14	0.15	0.16	0.16	0.17	0.18	0.19	0.20	0.21
2.7	0.45	0.10	0.11	0.12	0.13	0.14	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.21
2.8	0.45	0.10	0.11	0.12	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.21
2.9	0.44	0.10	0.10	0.11	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.21
3.0	0.43	0.09	0.10	0.11	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.20	0.21

Appendix Table B-3 (cont'd). Calculated optimal relative recruitment length (L_m) and fishing mortality (F) for M/K ratios in the range 0.2-3.0 and natural mortality rates (M) in the range 0.1-0.35. L_m is expressed as a decimal fraction of L_∞.

		Natural mortality (M) values												
M/K	L_∞	0.23	0.24	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.34	0.35
0.2	0.86	0.41	0.42	0.44	0.46	0.48	0.49	0.51	0.53	0.55	0.57	0.58	0.60	0.62
0.3	0.83	0.38	0.40	0.42	0.43	0.45	0.47	0.48	0.50	0.52	0.53	0.55	0.57	0.58
0.4	0.80	0.36	0.38	0.39	0.41	0.43	0.44	0.46	0.47	0.49	0.50	0.52	0.54	0.55
0.5	0.78	0.34	0.36	0.37	0.39	0.40	0.42	0.43	0.45	0.46	0.48	0.49	0.51	0.52
0.6	0.75	0.33	0.34	0.36	0.37	0.39	0.40	0.42	0.43	0.44	0.46	0.47	0.49	0.50
0.7	0.73	0.32	0.33	0.34	0.36	0.37	0.38	0.40	0.41	0.43	0.44	0.45	0.47	0.48
0.8	0.71	0.30	0.32	0.33	0.34	0.36	0.37	0.38	0.40	0.41	0.42	0.44	0.45	0.46
0.9	0.69	0.29	0.31	0.32	0.33	0.34	0.36	0.37	0.38	0.39	0.41	0.42	0.43	0.45
1.0	0.67	0.28	0.30	0.31	0.32	0.33	0.34	0.36	0.37	0.38	0.39	0.41	0.42	0.43
1.1	0.65	0.27	0.29	0.30	0.31	0.32	0.33	0.35	0.36	0.37	0.38	0.39	0.41	0.42
1.2	0.63	0.27	0.28	0.29	0.30	0.31	0.33	0.34	0.35	0.36	0.37	0.38	0.40	0.41
1.3	0.61	0.26	0.27	0.28	0.30	0.31	0.32	0.33	0.34	0.35	0.36	0.37	0.39	0.40
1.4	0.60	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.34	0.36	0.37	0.38	0.39
1.5	0.58	0.25	0.26	0.27	0.28	0.29	0.30	0.32	0.33	0.34	0.35	0.36	0.37	0.38
1.6	0.57	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.34	0.35	0.36	0.37
1.7	0.56	0.24	0.25	0.26	0.27	0.28	0.29	0.31	0.32	0.33	0.34	0.35	0.36	0.37
1.8	0.54	0.24	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.34	0.35	0.36
1.9	0.53	0.24	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.34	0.35	0.36
2.0	0.52	0.23	0.24	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.35	0.36
2.1	0.51	0.23	0.24	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.34	0.35
2.2	0.50	0.23	0.24	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.34	0.35
2.3	0.49	0.23	0.24	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.34	0.35
2.4	0.48	0.23	0.24	0.25	0.26	0.27	0.28	0.28	0.29	0.30	0.31	0.32	0.33	0.34
2.5	0.47	0.22	0.23	0.24	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.34
2.6	0.46	0.22	0.23	0.24	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.34
2.7	0.45	0.22	0.23	0.24	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.34
2.8	0.45	0.22	0.23	0.24	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.32	0.33	0.34
2.9	0.44	0.22	0.23	0.24	0.25	0.26	0.27	0.28	0.29	0.30	0.31	0.31	0.32	0.33
3.0	0.43	0.22	0.23	0.24	0.25	0.26	0.27	0.27	0.28	0.29	0.30	0.31	0.32	0.33

Appendix F. Glossary of symbols.

a mathematically fitted parameter of the weight-length function

α a parameter of the Shepherd (1982) stock-recruit function representing the survival from egg to age 1; also a dimensionless parameter of the Ricker stock-recruit function (see page 282 of Ricker (1975)

A annual (total) mortality rate

b mathematically fitted parameter of the weight-length function

β parameter of the Shepherd stock-recruit function which adjusts the rate at which early survival decreases as population density increases

CV coefficient of variation

f fecundity (eggs per kg of mature female biomass)

F instantaneous rate of fishing mortality

$F_{0.1}$ fishing mortality rate where the marginal yield per recruit is 10% of the marginal yield per recruit with little fishing

F_{ext} the level of fishing mortality just sufficient to drive the population to extinction

F_{msy} fishing mortality rate that produces MSY for a population

K von Bertalanffy growth parameter

K′ an estimate of K derived using an empirical estimate of L_∞

K in the Shepherd stock-recruit relation, an adult biomass above which density effects on early survival dominate

L fork length

L_c optimal length at recruitment

L_∞ asymptotic length, a von Bertalanffy growth parameter

L_∞' an empirically derived estimate of L_∞

L_t fork length at age t

M instantaneous rate of natural mortality

MSY maximum sustainable yield

p probability

R number of recruits at age 1

S biomass of mature females at spawning time

SY sustainable yield (kg ha^{-1} yr^{-1})

T annual mean temperature ($^{\circ}C$) of the water in which a stock lives

THV thermal habitat volume (cubic hectometres per 10 d)

t_0 extrapolated age at which $L_t = 0$

W weight (g)

Z instantaneous rate of total mortality